Perception of emotions from faces and bodies and the influence of context

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PERCEPTION OF EMOTIONS FROM FACES AND BODIES AND THE INFLUENCE OF CONTEXT

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"Every phase of movement, every small transference of weight, every single gesture of any part of the body reveals some feature of ... inner life."
~ Rudolf Laban ~

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Chapter 1

General introduction

" Pour rêver, il ne faut pas fermer les yeux, il faut lire. La vrai image est connaissance. "
~ Michel Foucault (1967) ~

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In everyday life, we are continuously confronted with other people. How they behave and move around has a direct influence on us whether we are aware of it or not. In communication, we are generally focused on the face. For this reason, emotion research in the past has focused on faces. Also, facial expressions seem to have universal consistency. However, bodily expressions are just as well recognized as facial expressions, they can be seen from a distance and are from evolutionary perspective much older. Body language therefore has a high communicative role albeit we are less aware of it. Models on facial expression processing might also work for understanding bodily expressions. Similar brain regions seem to get activated for both, but although faces show the mental states of people, body postures in addition show an action intention.

In a naturalistic environment, faces never appear alone: they are mostly always accompanied by a body which influences how the facial expression is perceived. This is also the case for other modalities such as the voice. Which modality is dominant depends on the specific emotion being shown, on the situation and many other factors. For example, aggression seems to be more pronounced in bodily expressions, while shame or disgust can clearly be seen from the face. Also the context, including other people or not, can facilitate recognition of emotions. Moreover, we do not live in a static world; dynamic stimuli give us, just like in the real world, more information. Body language of people interacting can tell us much about their relationship.

The nature of emotion perception cannot be fully understood by focusing separately on social, cultural, contextual, individual or interpersonal factors. The percept of an emotion is embodied, and its bodily-grounded nature provides a foundation for social communication. Furthermore, perception and recognition of bodily expressions does not require full attention nor does it require that the visual stimulus is consciously seen. For example, brain areas involved in emotion will respond to angry faces that are briefly presented and then rapidly masked, even when subjects are unaware of having seen the face.

These topics will be discussed in this thesis. They show us that being able to recognize emotional meaning from others is vital and that body language is of crucial importance in normal communication. This is clearly impaired in disorders such as autism. Therefore, investigations of bodily expressions will enrich basic clinical research and can lead to the development of new observational and diagnostic tools.

Mechanisms of emotion

For decades, psychologists had been puzzled about what was called the primacy debate. When we encounter a bear in the forest, do we feel fear because our heart rate increases, or does the fearful experience lead to the increased heart rate? The

former was believed to be the case by James and Lange (1884): the experience of an emotion depends on behavioral and bodily reactions following a specific event. However, getting angry also increases your heart rate. The existence of common physiological responses for different emotions – although we now know there are slight differences – led Cannon and Bard in the 1920s to suggest that autonomic arousal and the emotional experience arise simultaneously in the individual. They did not give an explanation for what distinguishes one emotion from another. Schachter and Singer (1960s) believed this to be achieved by cognitive appraisals: The individual emotional experience gets colored by previous experience, expectations, and the situational context.

But what is the function of emotions? Darwin published in 1872 an important book on the evolution of emotion: 'The expression of emotions in man and animals.' In it, based on his own observations and reports from friends traveling the world, he argued that the expression of basic emotions is not only similar across cultures, but even across all mammals. He suggested that those expressions are evolved from behaviors that indicate what an animal is likely to do next. This has great communicative value on which other animals can react appropriately. Those action tendencies are according to Frijda (1986) actually the main feature of emotion. By this, emotions also have a motivational function, since unpleasant feelings give the need to take action to get rid of it.

For human facial expressions, Ekman and Friesen (1971) concluded that there are six basic emotions: surprise, anger, sadness, disgust, fear, and happiness. Whether the same basic emotions are present in the body is not clear yet. The studies in this thesis will mainly focus on the emotions fear and anger, which both signal a threat.

Brain mechanisms of emotion

Since all animals seem to have basic expressions of emotion, there must be a common mechanism in the brain. Indeed, in 1937 Papez proposed that emotional expression in humans is controlled by an evolutionary old part of the brain; several interconnected neural structures that he referred to as the limbic system, including hippocampus, mammilary body, anterior nuclei of the thalamus, and cingulate cortex. This model was later extended by MacLean by adding amygdala (AMG), hypothalamus, prefrontal cortex, and association cortex.

The AMG, an almond-shaped nucleus in the middle anterior temporal lobe, is a very important structure in this system. Cognitive elements in emotion are mediated by pathways from the AMG to the cerebral cortex, where outcomes are evaluated or decisions can be made. However, emotional states are not only experienced consciously, but also unconsciously. The unconscious autonomic and endocrine

responses are mediated by subcortical nuclei from especially the AMG and hypothalamus to the brain stem, where information goes down the spinal cord to the rest of the body. Those autonomic responses prepare the body for action and by doing so at the same time provide information to other people or animals. This unconscious processing is also very important for making decisions based on 'gut feelings'. Work by Damasio on humans with frontal cortex lesions reveals that unconscious emotional processing is necessary for rational risk-based decision making.
Many years of emotion research have found that the AMG seems to play a special role in the detection of salient events (*e.g.* see review Costafreda *et al.*, 2008). It also plays a key role in fear conditioning, whereby in studies an unpleasant stimulus (a mild electric shock) is paired with *e.g.* a specific tone. After learning, merely the sound of that tone will lead to autonomic fear responses in the body (LeDoux, 1995). Bilateral amygdalectomized patients (patients whereby the AMG had been surgically removed) show besides a difficulty in fear conditioning several other emotion-related problems, like not being able anymore to recognize fearful faces as being fearful. In the literature there is a discussion about whether the AMG is able to respond to emotional events independent of attention, or even awareness. The issue about attention will be discussed in the Chapter 5 and 6 of this thesis.

Functional magnetic resonance imaging (FMRI)

All brain results described in this thesis are found by using fMRI. This brain imaging method measures brain activity indirectly and non-invasively. In contrast to structural MRI, present in most hospitals, whereby anatomical pictures are made, functional MRI makes it possible to detect dynamic changes in brain activation over time. Its signal is based on the fact that changes in the cellular activity in the brain always go together with changes in local blood flow.
Subjects lying in an fMRI scanner undergo a strong magnetic field (in this case three Tesla), which makes all hydrogen protons in the body align to this field. Short radio waves are then emitted making the protons line up in another direction, after which they return to their original position. This returning creates local energy fields which are picked up by the scanner.
When a specific part of the brain is active at a certain time, it consumes energy in the form of oxygen and glucose which is extracted from the blood. To keep up with the energy consumption, more blood with oxygenated hemoglobin flows to the activated brain area, leading to a surplus of oxygenated to deoxygenated hemoglobin. This ratio can be measured by the scanner because they have different magnetic properties: deoxygenated hemoglobin is paramagnetic, leading to magnetic inhomogeneities. By measuring the ratio of oxygenated to deoxygenated blood, called the blood

oxygenation level dependent (BOLD) signal, assumptions can be made about which areas are activated.
Because this process of building up the BOLD signal takes some time, the temporal resolution of fMRI is relatively low compared to other methods: four to ten seconds. On the other hand, the spatial resolution is very good; it can detect changes in the ratio of oxygenated to deoxygenated hemoglobin in the range of a few millimeters.

Similarities and differences in neurofunctional basis of faces and bodies

Since a few years the neural correlates of body shape (Downing *et al.*, 2001) and perception of bodily expressions (de Gelder *et al.*, 2004) are the focus of experimental investigations. Although more or less neglected in the past in favor of faces, it is now increasingly believed that the perception of bodies has a special influence on our behavior. To be able to do this, they must be distinctly processed from other objects. The major concept used to argue for the specificity of processing is that of configuration. There is clear evidence that both faces and bodies are processed configurally, as a whole, rather than as a collection of features. This has been shown with 'the inversion effect': recognition of faces and bodies presented upside-down is relatively more impaired than inverted objects (Reed *et al.*, 2003). Besides behaviorally, this effect can also be investigated psychophysically by looking at electrophysiological recordings. With electroencephalography (EEG), electrical activity coming from firing neurons is picked up at the scalp through electrodes. By averaging brain activity to certain events, event-related potentials (ERPs) are formed. One such ERP component is the N1 that is thought to reflect a late stage in the structural encoding of the visual stimulus (Bentin *et al.*, 1996; Eimer, 2000) and originates from the lateral occipitotemporal cortex which houses the fusiform gyrus (FG). In the case of face processing, the N1 peaks at a different latency (around 170 ms after stimulus onset and hence called the N170) than for objects. The latency of the N170 is delayed when presented faces are inverted, which shows the involvement of FG in processing faces configurally. The N1 peak for body processing also differs from objects; it ranges from 154 to 228 ms after stimulus onset (Gliga & Dehaene-Lambertz, 2005; Meeren *et al.*, 2005; Stekelenburg & de Gelder, 2004; Thierry *et al.*, 2006; van Heijnsbergen *et al.*, 2007) and it also shows an inversion effect. Does this mean there is no difference between face and body processing?
No, it does not. Although EEG has a very high temporal resolution and can therefore tell us a lot about the timing of processing, it is hard to link a specific brain area to the found activation. A method better suitable to do this is magnetoencephalography

(MEG). This was recently done for investigation of the earliest onset of the electrophysiological inversion effect for different stimulus categories (Meeren *et al.*, 2008). The authors indeed found that the cortical distribution of this early effect was highly category-specific. Different time courses of activation were observed in the common neural substrate in FG. Furthermore, faces activated the inferior occipital gyrus (IOG; also named occipital face area (OFA)), whereas for bodies the effect was observed in the posterio-dorsal medial parietal areas (precuneus / posterior cingulate). Hence, whereas face inversion modulates early activity in face-selective areas in the ventral stream, body inversion evokes activity in dorsal areas, suggesting different early cortical pathways for configural face and body perception.
Besides this early processing in perceiving faces and bodies, more general processing on longer time scales can be investigated with fMRI. With this method, there has actually been found a distinction in the FG between faces and bodies, thereafter called fusiform face area (FFA) and fusiform body area (FBA) (Schwarzlose *et al.*, 2005). Furthermore, bodies seemed to be processed also in another area: the extrastriate body area (EBA) (Downing *et al.*, 2001). This area lies very close to the human motion area (hMT+/V5), and given that bodies imply action, this finding is not peculiar. Besides, superior temporal sulcus (STS) and premotor cortex (PM) also get activated for bodies (Grèzes *et al.*, 2007), the former is known to be involved in biological motion (Bonda *et al.*, 1996), the latter also being a motor area.
When directly comparing the neural correlates of faces and bodies, the sparse evidence points to a broader network for the perception of bodies, probably due to the action component involved in those. It is remarkable that the literature on isolated face and body perception is more extensive compared to the knowledge of the more ecologically valid combined perception of a face on a body. The few studies available addressing this issue consistently point to a strong mutual influence (Aviezer *et al.*, 2008; Meeren *et al.*, 2005; Van den Stock *et al.*, 2007).

Emotional modulation of body selective areas

That faces and bodies are processed in a distinct way, being special classes of objects, has probably to do with their ecological value. We are experienced in recognizing many different facial identities and being able to react appropriately to intentions stated in bodies has survival value. Important sources of information about someone's intentions are facial and bodily expressions. Being able to quickly react to these, they must be effectively processed in the brain.
Evidence was found for fast automatic processing of emotional body language. Fear expressed by the body affected the response of the P1 component already at 100-120 ms after stimulus onset and also the N170 component showed a difference (van

Heijnsbergen *et al.*, 2007). This means that processing of the emotion goes faster than identifying a body.
This emotional processing partly takes place in the face and body areas, suggesting a better representation of the faces and bodies. Several studies have reported emotional modulation of face selective areas fusiform face area (FFA) and occipital face area (OFA) (Breiter *et al.*, 1996; van de Riet *et al.*, 2009; Vuilleumier *et al.*, 2001). However, this effect may be dependent on age (Guyer *et al.*, 2008), attachment style (Vrticka *et al.*, 2008), personality type, and gender of the observer and the observed (Kret *et al.*, 2011a). So far, only a few studies investigated the effects of emotional information of body expressions on activation of body areas in the brain. The first fMRI study addressing this issue observed an increased activation of FG and amygdala (AMG) for fearful body expressions (Hadjikhani & de Gelder, 2003). A follow up experiment showed additionally the involvement of motor areas (de Gelder *et al.*, 2004). Also when directly comparing neutral and emotional faces and bodies (van de Riet *et al.*, 2009), it was observed that emotional bodies activate (sub) cortical motor related structures, such as the inferior frontal gyrus (IFG), caudate nucleus and putamen which has probably to do with being able to respond fast to emotional bodies.
Although the findings of emotional modulation of FBA have been replicated (Peelen *et al.*, 2007), emotional modulation of EBA is uncertain. No difference was observed between neutral and emotional body images (van de Riet *et al.*, 2009) but data with dynamic body expressions does show emotional modulation (Grèzes *et al.*, 2007; Kret *et al.*, 2011b; Pichon *et al.*, 2008; Sinke *et al.*, 2010).

Affective gist of the scene influences the perception of emotions

Normally, we do not see isolated people, but we see them in a context. How does this influence our percept of the bodily expression of a single individual?

■ Emotional context

Because of repetitive co-occurrence of objects or co-occurrence of a given object in a specific context, our brain generates expectations (Bar & Ullman, 1996; Palmer, 1975). A context can facilitate object detection and recognition (Boyce *et al.*, 1989; Palmer, 1975), even when glimpsed briefly and even when the background can be ignored (Davenport & Potter, 2004). Joubert and colleagues (2008) also observed that context incongruence induced a drop of correct hits and an increase in reaction times, thus affecting even early behavioral responses. They concluded that object

and context must be processed in parallel with continuous interactions possibly through feed-forward co-activation of populations of visual neurons selective to diagnostic features. Facilitation would be induced by the customary co-activation of "congruent" populations of neurons whereas interference would take place when conflictual populations of neurons fire simultaneously. Bar (2004) proposes a model in which interactions between context and objects take place in the inferior temporal cortex.

Just like recognizing objects is not independent from other cues such as context, emotion perception does not proceed on information from one cue (as facial expressions) alone (Hunt, 1941). Knowledge of the social situation (Aviezer *et al.*, 2008; Carroll & Russell, 1996), body posture (Meeren *et al.*, 2005; Van den Stock *et al.*, 2007), other emotional faces (Russel & Fehr, 1987), voice (de Gelder & Vroomen, 2000) or linguistic labels (Barrett *et al.*, 2007) influence emotion perception and even which emotion is seen in the structural configuration of the participants' facial muscles. In line with the evolutionary significance of the information, the effects of the emotional gist of a scene may occur at an early level. Previously, scene context congruency effects on facial expressions were shown in behavioural responses but also in EEG measurements; It could be observed when participants had to explicitly decode the emotional expression of the face (Righart & de Gelder, 2008) but also when they focussed on its orientation (Righart & de Gelder, 2006). This indicates that it reflects an early and mandatory process and suggests a perceptual basis. Looking at EEG, it can be seen that the presence of a fearful expression in a fearful context enhanced the face-sensitive N170 amplitude as compared to a face in a neutral context. This effect was absent for contexts-only, indicating that it resulted from the combination of a fearful face in a fearful context (Righart & de Gelder, 2006). That scenes are indeed important is also shown in two recent fMRI studies where participants interpreted facial expressions differently and different brain areas were activated depending on the context (Kim *et al.*, 2004; Mobbs *et al.*, 2006).

■ Social emotional context

Does it influence our emotional reaction when we watch a single individual fleeing from danger while bystanders are passively standing there? Do we ignore the social scene to focus only on the emotion of the target figure or are we unwittingly influenced by the social scene viewing individual action through the filter it provides us? Studies on crowd behavior (McDougall, 1920) indicate that social scenes provide a context in which individual actions are better understood prompting an adaptive reaction in the observer. Using point-light displays, Thornton and Vuong (2004) have shown that the perceived action of a walker depends upon actions of nearby "to-be-ignored" walkers. Another point-light study by Clarke and colleagues (2005) demonstrates that the recognition of a person's emotional state depends upon another person's presence (Clarke *et al.*, 2005). A recent study by (Kret & de Gelder,

2010) reports that the social group in which we encounter a person, and especially their bodily expressions, influence how we perceive the body language of this single individual. In this study, images of emotional body postures were briefly presented as part of social scenes showing neutral or emotional group actions. These were more accurately and faster recognized when the actions in the scenes expressed an emotion congruent with the bodily expression of the target figure.

These studies show the importance of a social (emotional) scene. However, other processes than the ones measured may contribute to the observed effects, for example the tendency to automatically mimic and synchronize facial expressions, vocalizations, postures, and movements with those of another person and to converge them emotionally (de Gelder *et al.*, 2004; Hatfield *et al.*, 1994). Similar brain areas are involved when subjects experience disgust (Wicker *et al.*, 2003) or pain (Jackson *et al.*, 2005), as when they observe someone else experiencing these emotions. Such a process may contribute to observers' ability to perceive rapidly ambiguity between a person's body language and its social (emotional) context. Such incongruity may create a conflict in emotional contagion processes triggered by the target figure and help to explain the slower and less accurate reaction in the observer.

Static *vs.* dynamic

Research performed with facial and bodily pictures have contributed a lot to our understanding of how our brain processes these stimuli. However, in real life, we are confronted with moving people. Although static body postures already imply motion, dynamic stimuli obviously contain more information, which helps in better understanding someone's intentions and being able to react appropriately to these.

Point-light display studies showed that biological motion is quickly detected (Johansson, 1973). A few neuroimaging studies report the importance of movement in processing emotional expressions (see *e.g.* Decety & Chaminade, 2003; Grosbras & Paus, 2006; LaBar *et al.*, 2003). Adolphs *et al.* (2003) reported that a patient with a ventral pathway lesion is able to read emotion from dynamic, but not from static facial expressions (Adolphs *et al.*, 2003).

In healthy subjects, Sato *et al.* (2004) found that the AMG, IOG and FG were more activated by dynamic than static fearful facial expressions. Studies of bodily expressions also report better recognition rates for dynamic versus static stimuli (Atkinson *et al.*, 2004; de Meijer, 1989). A recent brain imaging study looked at the perception of angry and neutral hand and face movements (Grosbras & Paus, 2006). The authors reported that regions known to be involved in action and emotion generation in oneself also get activated when perceiving action and emotion in faces and hands of others. Furthermore, they reported an interaction between emotion

and body part: When hand actions were performed with emotion, a region in the supramarginal gyrus responded mostly to this. Since this region had been implicated before to be involved in getting attention towards a limb (Rushworth *et al.*, 2001), it seems here that the emotion in the hand movement increased this attention.
This study, however, was not designed to detect specifically what additional information is contributed by dynamics. Two studies that tried to do this used 3 sec videoclips of someone opening a door in either a neutral or in a fearful (Grèzes *et al.*, 2007) or angry way (Pichon *et al.*, 2008). From each movie, one frame at which the emotion was at its peak was taken and also presented for 3 sec. Not surprisingly, dynamic *vs.* static body expressions (irrespective of the emotional content) caused motor resonance: bilateral activations of PM and parietal cortex, STS and FG. Most interestingly, an interaction was observed between emotion and motion in STS and right PM. In humans, STS, parietal and PM are involved in action observation and probably also in action understanding (Grèzes & Decety, 2001), so since these areas represented the emotional action in this study, they could also be involved in emotion understanding.

Perceiving interactions

Trying to get additional information going from static to dynamic facial and bodily expressions and including a context, there is another step to take to get to even more naturalistic situations. This is the perception of a person interacting with another person. The interplay between those can inform us about their relationship.
Social interactions are part of our daily life. Almost all human activity involves other people or at least has in one way or the other consequences for other people. Because of this we are continuously aware of the social implications of our actions or how it may affect our social relations. This notion has led some authors to believe that humans have evolved the cognitive adaptation of processing social relations during slack time (Iacoboni *et al.*, 2004; Schilbach *et al.*, 2008). Some areas in the brain are tonically active when not doing any overt task, including medial parietal (precuneus) and dorsomedial prefrontal cortices, together called the default network. Those areas were found to get more activated when watching movies in which two people interact than passively watching other kind of stimuli including when the movies showed only one person performing a similar action (Iacoboni *et al.*, 2004). This led to the idea that thinking about social relations is a default state of the brain. That there has been found a difference in activity within this network between patients with social phobia and healthy controls implicates again its role in social processing (Gentili *et al.*, 2009). It is not a new notion that we have a predisposition towards automatically looking for social meaning; a study from the 40s showed that just watching moving

geometric shapes gives people the impression of animacy and social interaction (Heider & Simmel, 1944).
When similar movies recently were shown to participants during magnetoencephalography (MEG) measurements with the explicit instruction to look for social interactions, indeed brain regions involved in processing social interactions were found active, like temporoparietal junction (TPJ), fusiform face area (FFA), posterior superior temporal sulcus (pSTS) and medial prefrontal cortex (Pavlova, 2010). Those experiments imply that getting the impression of seeing social interaction from those simple shapes is induced by the motion. This shows the importance of using dynamic stimuli in research on this topic, which has been done in the experiments discussed in Chapters 5 and 6.

Bodies processed without attention and visual awareness

Studies with hemianopia patients already showed that perception or recognition of bodily expressions does not require full attention. Patients with striate cortex lesions or an attentional disorder can react to a visual stimulus even though they have not consciously seen it. Patients with left hemispatial neglect due to a lesion in the right parietal cortex fail to direct attention to stimuli in their left visual field. However, when the stimulus is an expressive in contrast to a neutral face or body or a neutral object, they are better able to perceive it.
The clearest example of being able to process emotional signals has been given by patients with lesions to their primary visual cortex (V1). Under stringent testing conditions, they were able to discriminate between visual properties of stimuli they can not consciously see. This phenomenon is called 'blindsight'. Later, it was shown that they were also able to guess correctly the emotional valence of facial stimuli presented in their blind visual field, so-called 'affective blindsight' (de Gelder *et al.*, 1999). In the first behavioral study only moving stimuli but not still images of facial expressions appeared to support affective blindsight. If movement was the critical aspect to support non-conscious discrimination of different emotional expressions, one would expect blindsight also for other attributes that rely on movement. However, blindsight was only observed for emotional facial expressions and not facial speech (de Gelder *et al.*, 2000). Other facial attributes such as personal identity or gender were also tested with negative results, suggesting that neither movement nor non-emotional facial attributes are per se determinants of the phenomenon. More directly, in later research affective blindsight emerged very clearly also when still images of facial expressions were used, especially when tested with indirect methodologies

(Anders *et al.*, 2004; Pegna *et al.*, 2005). Still unknown is whether affective blindsight is induced by non-conscious processing of overall face configuration or by individual key features. There is evidence that the eye region is most salient in conveying emotion information, and that the most ancient parts of our visual and emotion systems in the brain seem tuned to detect this simple signal rather than the whole face configuration (Kim *et al.*, 2004; Morris *et al.*, 2002).

Aside from facial expressions, other stimulus categories have been used to test whether affective blindsight could be extended to other stimuli. Thus far, the most studied categories are affective scenes and bodily expressions. Generally, negative results have been reported for scenes, suggesting that the appraisal of the emotional content of complex pictures requires cognitive and semantic processing that depends on conscious visual perception (de Gelder *et al.*, 2002). On the other hand, behavioral and neuroimaging results have shown that affective blindsight for bodily expressions may be at least as clearly established as that previously reported for facial expressions, and sustained by a partly overlapping neural pathway (de Gelder & Hadjikhani, 2006). This implies that implicit processing of emotions in blindsight is non-specific for faces but for biologically primitive emotional expressions in general.

For the studies in this thesis, only healthy students were tested. Stimuli were presented long enough to be consciously seen. Therefore, 'automatic' processing of bodily expressions was only being investigated by showing stimuli of social interactions while participants were given an unrelated task.

Research aims and thesis outline

Previous emotion research has mainly focused on the perception of facial expressions. Only in recent years, bodily expressions are being studied. This has been done by using pictures of isolated bodies. However, in our daily life, bodies are not static and do not appear in isolation. Therefore, the stimuli used in Chapter 5 and 6 are dynamic. There is reason to believe that the perception of faces and bodies might be influenced by the context it is in. This can be the physical environment, the culture, or other people. The question therefore is how a face or a body, being emotional or not, is processed differently in specific contexts. Since everything that we do involves in some way other people, it is interesting to find out how the brain responds to an interaction between two people and whether it notices subtle differences in body language that can indicate whether a threat is going on. A final question was how attention can play a role in this perception.

Across cultures the expression of basic emotions is remarkably similar. However, emotion perception can be influenced by other factors, like the (social) context. Whether people from different cultures are differently influenced by this will be discussed in Chapter 2. More specifically, Dutch and Chinese students were tested on whether they show differences in the recognition of facial but also bodily expressions and whether they are differently influenced by context. The studies described in this chapter are purely behavioural.

Moving away from cultural differences, in Chapter 3 the influence of context on face processing is investigated using fMRI. Chapter 4 elaborates on the data from this study. Here, the activation of extrastriate body area is discussed in relation to its response to threatening scenes specifically.

The study performed in Chapter 5 moves from static pictures to dynamic movies of two people interacting. This interaction was either threatening or teasing. A difference is made in whether participants actively try to guess what goes on in each situation or perform an unrelated task. Chapter 6 expands on perceiving threatening social interactions by using two different attention levels and letting the participant focus on only one of the two protagonists (always one of them being angry at the other) in each movie.

Finally, in Chapter 7, the insights gathered from the preceding chapters are summarized.

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Chapter 2

Cultural differences in recognition of facial and bodily expressions and contextual influence

" Ce sont dans les formes immobiles que les mouvements sont les plus faciles a saisir. "
~ Serge Gainsbourg ~

Chapter based on:
Sinke, C.B.A., Kret, M.E., Van den Stock, J. & de Gelder, B. Cultural differences in recognition of facial and bodily expressions and contextual influence. (submitted)

Abstract

It is generally agreed that cultural background plays a role in social interactions but studies on cultural factors influencing social and emotion processes are scarce and almost exclusively focused on facial expressions. Here we investigated the impact of ingroup vs. outgroup on recognition of face and whole body expressions in Dutch and Chinese participants. Results show that the worse recognition memory performance of Chinese vs. Dutch participants for Caucasian faces disappears when the faces carry an emotional expression. Furthermore, Chinese participants appear to be more specialized for faces than Dutch participants; they are better in recognizing both Chinese and Caucasian identities and they do this faster than identifying shoes or bodies. However, with emotional expressions, whether faces or bodies, Chinese participants are slower than the Dutch. Also, the Chinese participants need more time to recognize (emotional) bodies in a non-social context, but when bodies are perceived in a social context this difference disappears. At the same time, the Chinese group performs better, indicating the Chinese are more influenced by a social scene in general than are Dutch individuals. By focusing on bodily expressions and (non) social scenes in addition to isolated faces, this study gives further insight into cultural differences in emotion perception.

Introduction

With communication technologies and enterprises increasingly going global our interactions with people from different cultures become more important. For example, as has often been noted, correctly judging the intentions of your business partner can make the difference between reaching a lucrative deal or not. Likewise, if our communication with robots and avatars will be important in the future, interactive understanding of intentions and emotions is critical.

In the past, research on cultural differences has mainly focused on the face. This face-centrism is in line with the fact that face perception has been a topic of extensive research for the last decades (see *e.g.* (Adolphs, 2002; Ekman, 1982; Puce *et al.*, 1996)). A small number of studies have looked at the role of race asking whether people perceive faces from their own race differently than faces of other races. Evidence indicates that people are better in recognizing faces from their own race than faces from other racial groups (Lindsay *et al.*, 1991; O'Toole *et al.*, 1994). Walker and Tanaka (2003), using a sequential matching task with natural and morphed East Asian and Caucasian faces, found this race effect already at early stages of perceptual encoding (Walker & Tanaka, 2003). An event-related potential known to be specifically involved in face processing, the N170 (Eimer, 2000), showed a larger

amplitude for Asian than Caucasian faces in Caucasian subjects but there was no effect in the earlier P100 component which has been related previously to processing of the emotional expression (Batty & Taylor, 2003; Herrmann *et al.*, 2007). This may indicate that a race effect becomes present at a late stage of structural visual encoding of the face.

The studies mentioned so far investigated facial identity recognition. Yet emotions play a big role in communication and culture provides unwritten interpersonal rules about how to deal with these. For example, in some cultures hierarchy is much more important than in others and people from lower levels are not supposed to show their emotions. Because of these traditions, people in East Asian countries, for example, are in general more emotionally introvert. So emotions are also not always expressed similarly or in the same degree across different countries. Probably because of these differences in expression, there are also subtle differences in how people from different countries interpret emotions (Elfenbein & Ambady, 2002). The voice also provides a context in which the face is perceived and cultural differences have also been reported on the combined perception of faces and voices. It has been shown that Japanese – in contrast to Dutch – participants are influenced by the affective information in the voice when rating facial expressions (Tanaka *et al.*, 2010).

While there is little doubt that the face can tell a lot about someone's feelings or intentions, it is also obvious that body language is also an equally important indicator. Bodily expressions of emotion are only a recent domain of interest but knowledge in this area is increasing (see (de Gelder, 2006, 2009; de Gelder *et al.*, 2004) for reviews). However, cultural differences in perceiving bodily expressions have been studied sparsely. So far there has been only one study: short movie clips of ten basic Hindu emotions expressed by face and body in classical Indian dance were presented to American and Indian students (Hejmadi *et al.*, 2000). With forced response alternatives, both groups performed equally well. However, there was a significant difference between groups when the task was to freely describe emotions.

A third important point is that faces and bodies are normally observed as part of a real life context, which can already give an indication about the meaning of a person's expression. Whether indeed there are cultural differences in the influence of surrounding people's emotion on the perception of a face was tested by Masuda *et al.* (2008) who let Japanese and Caucasian participants rate the emotion of a face in a social context. The results showed a social context influence on the emotion perception of the target face, but only for the Japanese participants. Eye-tracking data showed that Japanese subjects looked more at the context than Western participants (Masuda *et al.*, 2008).

In the present study, we investigated a number of novel issues about cross-cultural emotion perception. Our first issue concerned whether the other race effect, the well-known difference in recognition memory for other race faces, will be influenced by emotion. Secondly, we wanted to replicate previous findings that people are better

able to identify faces from their own than from another race. Thirdly, we investigated body expressions and tested Chinese and Dutch participants on recognition of facial and whole body expressions. Finally, we addressed the role of social context and investigated cultural differences in sensitivity to the social context.

Methods and results

■ Participants

Twenty-two Chinese students (13 males; 22.2±0.9 years) and 24 Dutch students (8 males; 18.4± 3.2 years) participated in this study. All were right-handed and had (corrected to) normal vision. They gave written informed consent and were paid for their participation. The Dutch students only participated in the six match-to-sample tasks; for the recognition memory tests and both emotional body judgment tasks, the Chinese data was compared with the data from other Dutch students (see (Kret and de Gelder, 2010) for the social contexts (21 participants) and (Van den Stock, Sinke, and de Gelder, submitted) for the non-social contexts (16 participants; recognition memory: 21 participants) who were tested recently before in the same lab.

Our Chinese participants were tested within two weeks of arriving in the Netherlands, so they had not had intensive contact yet with Caucasian individuals. For most of them, this was their first time abroad; only four students (18.2%) had been on an exchange to Europe/ the US for ten days to maximally four months (on average 1.8 months).

■ Materials

The different tests used in this study have all been validated and used before in different experiments within our lab (see (de Gelder *et al.*, 1998; Kret & de Gelder, 2010; Van den Stock *et al.*, to be submitted)).

■ Design and procedure

Participants were comfortably seated in a dimly lit room. English instructions were given verbally and on the screen. All stimuli were presented on a monitor with a refresh rate of 60 Hz using E-Prime (Version 10.2) with the exception of the experiment using bodies in a non-social context where Presentation (Neurobehavioral Systems, Inc, version 11.0) was used. We used a number of different face and body experiments in order to probe different aspects of face recognition and emotion recognition in faces and bodies. Total time of all experiments together was 64 minutes. Viewing distance was ~ 60 cm.

Facial memory was tested for neutral faces or for emotional faces by using an adapted version of the Warrington Recognition Memory for Faces Test (Warrington,

1984). Subjects were presented with 50 faces for 3s each in the training phase. In the subsequent test phase, two faces were shown simultaneously and participants had to indicate by a button press (no time limit was given) which of the two faces had already been shown in the test phase. We developed the same test this time using emotional faces. Subjects were shown unfamiliar faces with one of three facial expressions and in the test phase always two faces with the same emotion were shown and subjects were instructed to respond which of the two individuals they had seen during the preceding training phase. No mention was made of the facial expression. For these tests, we looked only at accuracy rates (ACCs) and not at reaction times (RTs).

Other experiments consisted of match-to-sample tasks, each lasting about three minutes. There were six of these and they involved matching Caucasian faces by identity, Chinese faces by identity, shoes by identity, Caucasian faces by emotion, bodies by emotion and bodies by (emotionally neutral) action. The shoe identity task served as control for general performance during a match-to-sample task. During all match-to-sample tasks always one picture was presented on top which had to be matched with one of the two pictures below. For the identity tasks this meant that the view from the face/shoe pictures below were turned 45°. The stimuli were presented until a response was given.

In two additional tasks, participants had to judge (emotional) bodies in a non-social (Van den Stock *et al.*, to be submitted) and social context (Kret & de Gelder, 2010). Stimuli from the first experiment were presented for 800ms with the next picture presented 500ms after responding to the previous. For the latter, stimulus presentation was 100ms. Since for this experiment we were only interested in recognizing bodily expressions, all faces (so from both the target figure and from the figures in the scene) were blurred. Finally, to be sure all participants correctly recognized the emotion of the social context; all pictures without central figure were shown for 1s for which participants had to judge the emotion.

An overview of the conditions and number of trials in each experiment can be found in table 1. The order of task administration was randomized between subjects.

Table 1. *Overview of the experiments.*

EXPERIMENT		Number of trials
1	Recognition memory test for neutral faces	50
2	Recognition memory test for emotional faces	50
3	Caucasian face identity matching	64 (16*4)
4	Chinese face identity matching	64 (16*4)
5	Shoe identity matching	64 (16*4)
6	Caucasian face emotion matching	60 (6 emotion categories (anger, disgust, fear, happy, sad, surprised) x 5 distracter categories x 2 genders)
7	Body emotion matching	24 (4 emotion categories (anger, fear, happy, sad) x 3 distracter categories x 2 genders)
8	Body action matching	60 (6 action categories (like *combing hair* or *pouring drink*) x 5 distracter categories x 2 genders)
9	Bodies in nonsocial contexts	288 (144*2) neutral/fearful body in neutral/fearful/ scrambled scene
10	Bodies in social contexts	512 (main: 256*2) fearful/happy body in fearful/ happy/neutral/scrambled scene 64 (recog: 32*2)

■ Data analysis and results

Recognition Memory Test for neutral faces

Two Chinese subjects who scored at chance level were excluded. For the same reason, one Dutch subject was excluded in addition to two subjects who had many missing data. An independent-samples t-test was performed to compare both groups. This showed a difference between groups ($t(35)=-2.276$, $p=.029$, $d=-.753$), Dutch subjects being more accurate than Chinese. Mean ACC was 80.0% (SD=.081) for Chinese and 86.7% (SD=.097) for Dutch participants. See figure 1.

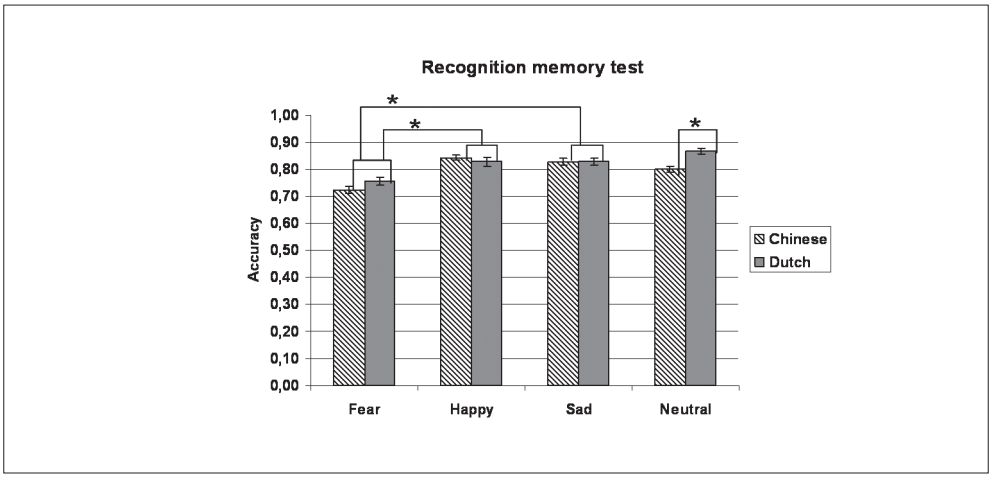

Figure 1. *Recognition memory test for emotional and neutral faces.*

Recognition Memory Test for emotional faces

No subjects were excluded from the analysis. A 2 (group: Chinese/ Dutch) x 3 (emotion: fear/ happy/ sad) ANOVA was performed.
The 2x3 ANOVA showed a main effect of emotion ($F(1,38)=15.682$, $p=.000$, $\eta p2=.452$), caused by a difference between fear and happy and between fear and sad. There is no group effect ($F(1,39)=.025$, p=n.s., $\eta p2=.001$). For Chinese participants mean ACC was 72.5% (SD=0.122), 84.3% (SD=0.098) and 83.0% (SD=0.118) for fear, happy and sad respectively. For Dutch participants this was 75.7% (SD=0.133), 82.9% (SD=0.146) and 82.9% (SD=0.128). See figure 1.

Match-to-sample tasks

Per subject, trials in which the RT exceeded 2 standard deviations (SDs) from the average were treated as outliers and were excluded from analysis. Average ACC and RT were calculated and first compared per task between both groups (Chinese/Dutch) by means of independent-samples t-tests. The only difference found in ACC between both groups was for the Chinese face identity task: Chinese were more accurate than Dutch participants ($t(43)=2.676$, $p=.011$, $d=.813$). However, there was also a trend for the same effect on the Caucasian face identity task ($t(43)=1.503$, $p=.143$, $d=.502$). RTs showed that except for the two face identity tasks, Chinese participants are slower than Dutch participants (shoe identity ($t(43)=3.208$, $p=.003$, $d=1.007$); Caucasian face emotion ($t(43)=2.814$, $p=.007$, $d=.887$); Caucasian body emotion ($t(43)=2.212$, $p=.032$, $d=.663$); Caucasian body action ($t(43)=2.732$, $p=.010$, $d=.901$), see figure 2).

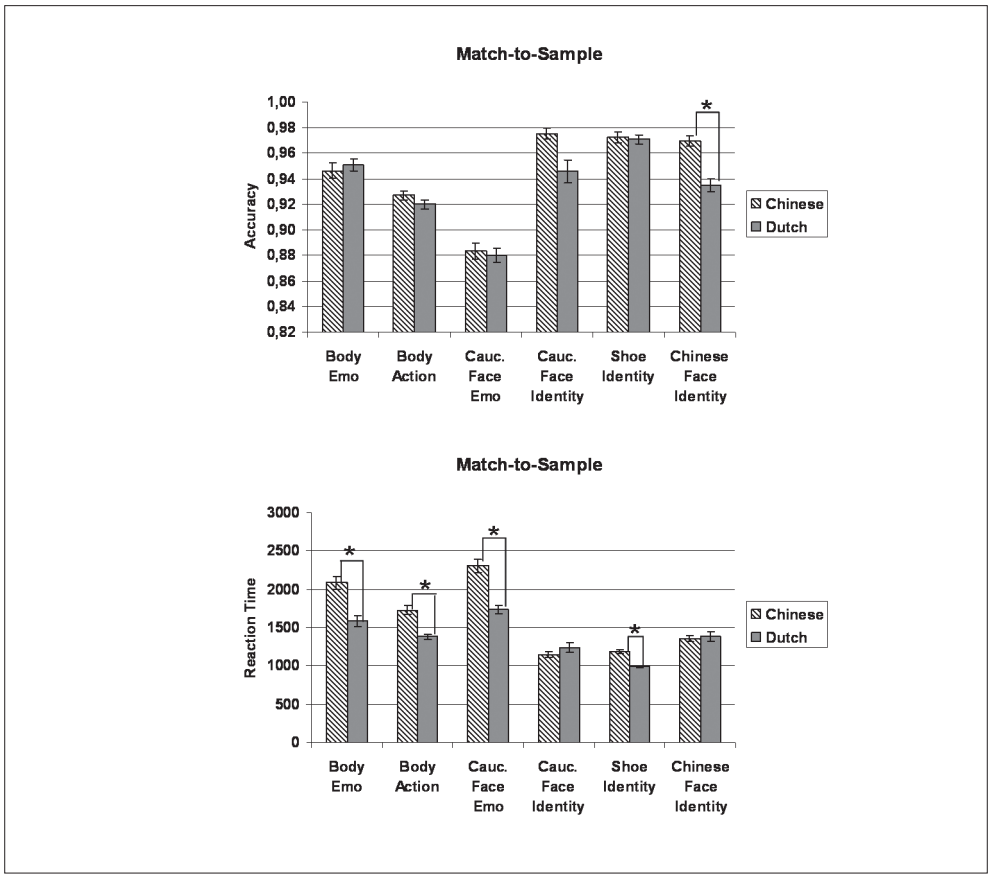

Figure 2. *Accuracy rates and reaction times in the match-to-sample tasks.*

We then looked specifically into the performance on identity matching of both Chinese and Caucasian faces to see whether we observed another race advantage using a 2x2 repeated measures ANOVA with group (Chinese/Dutch) as between-subject and identity (Chinese/Caucasian face) as within-subject factor. There was a group difference on the face identity tasks for ACCs ($F(1,43)=5.277$, $p=.027$, $\eta p2=.109$), Chinese being more accurate than Dutch. The RTs showed a main effect of identity: both groups are slower on the Chinese than Caucasian face identity task ($F(1,43)=17.437$, $p=.000$, $\eta p2=.289$). See figure 3.

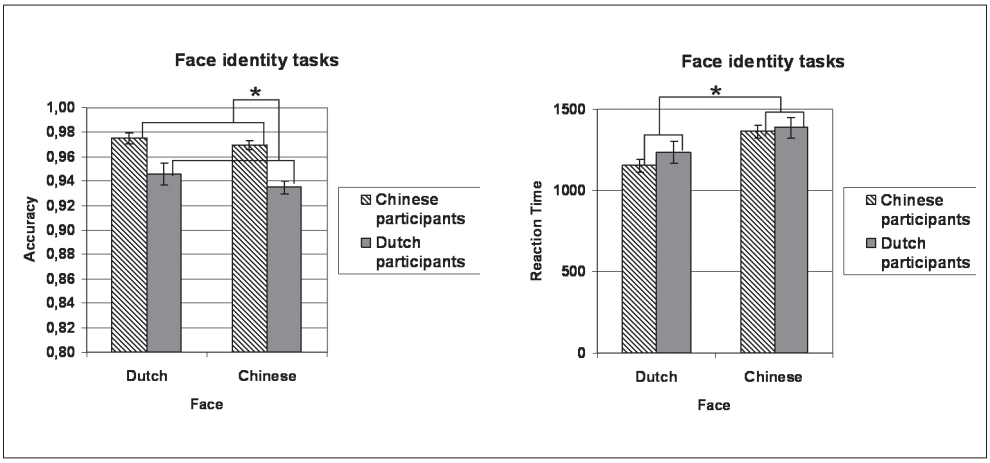

Figure 3. *Accuracy rates (showing a group difference) and reaction times (showing a main effect for face identity) in the face identity tasks.*

Second, to assess recognition of facial expressions in the Chinese group, we performed a 2x6 repeated measures ANOVA with as within-subject factor facial emotion (anger/disgust/fear/happy/sad/surprised) and between-subject factor group (Chinese/Dutch), followed by an independent-samples t-test. There was a facial emotion effect (F(5,215)=68.484, p=.000, ηp2=.614) for ACC which seems mainly caused by fear and surprise, both less accurately recognized than the other emotions. For RTs, there was a facial emotion x group interaction (F(5,215=3.853, p=.002, ηp2=.082), a main effect of facial emotion (F(5,215)=26.211, p=.000, ηp2=.379; both groups being fastest for happy faces) and a group effect (F(1,43)=8.323, p=.006, ηp2=.162; Chinese being slower than Dutch participants). Independent-samples t-test showed that the Chinese students are slower than Dutch on all emotions, except for happy (t(43)=1.385, p=n.s., d=.420). See figure 4.

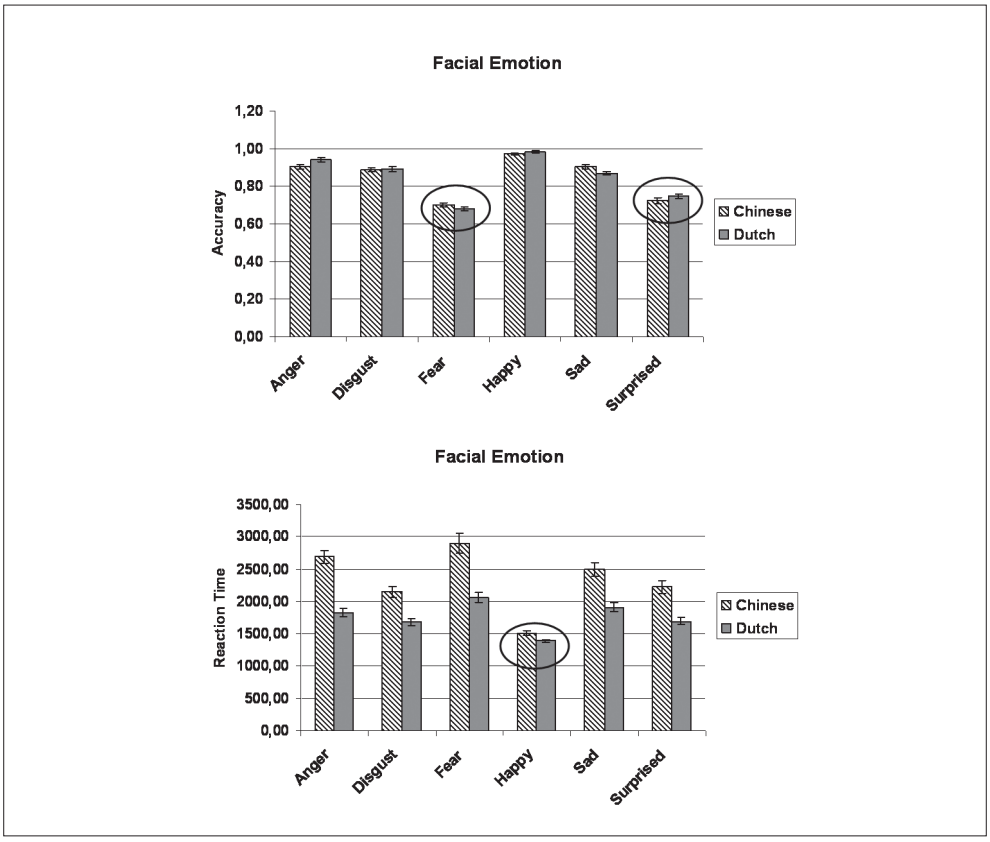

Figure 4. *Accuracy rates (showing an emotion effect) and reaction times (showing an emotion x group interaction and main effect for emotion) for facial emotion.*

Third, we wanted to know how well the Chinese group recognised Caucasian bodily expressions using a 2x4 repeated measures ANOVA with as within-subject factor bodily emotion (anger/fear/happy/sad) and as between-subject factor group (Chinese/Dutch). See figure 2 for an overview of the independent-samples t-tests all match-to-sample tasks together. We found a main effect of bodily emotion ($F(3,129)=10.547$, $p=.000$, $\eta p2=.197$), seemingly caused by sad which had in both groups a recognition rate of 100%. The RTs also showed a main effect of bodily emotion ($F(3,129)=20.425$, $p=.000$, $\eta p2=.322$), again probably caused by sad for which participants were fastest, and a group effect ($F(1,43)=4.925$, $p=.032$, $\eta p2=.103$): Chinese participants showed a higher reaction time than Dutch. See figure 5.

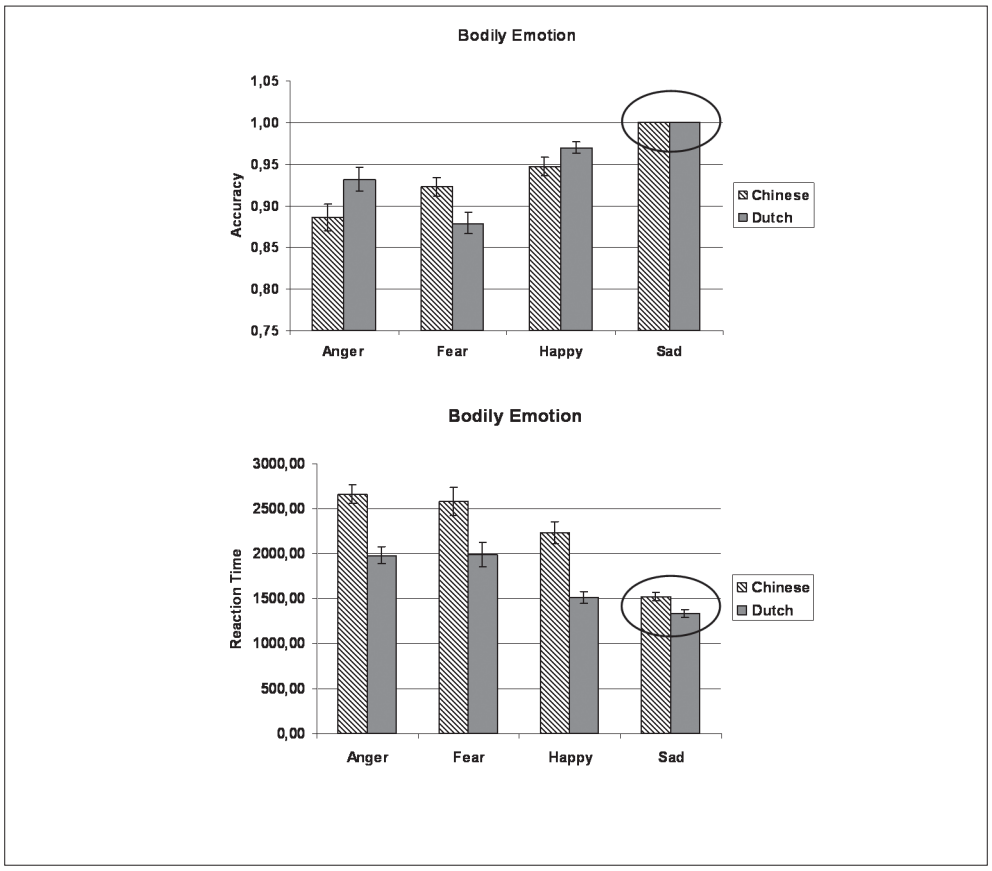

Figure 5. *Accuracy rates (showing a main effect of emotion) and reaction times (showing a main effect for emotion) for bodily emotion.*

Bodies in non-social contexts

We performed a 2 (group: Chinese/Dutch) x 2 (body: fear/neutral) x 3 (scene: fear/neutral/scrambled) repeated measures ANOVA with as between-subject factor group (Chinese/Dutch) for both ACCs and RTs. Also, an independent- and paired-samples t-test was performed to look into interaction effects.

The 2x2x3 ANOVA on ACC data showed a bodily emotion x group interaction ($F(1,72=4.261$, $p=.046$, $\eta p2=.106$). However, the independent-samples t-test does not show any significant results. For RTs, there was a bodily emotion x scene ($F(2,35=3.733$, $p=.029$, $\eta p2=.094$) and a group ($F(1,36=4.796$, $p=.035$, $\eta p2=.118$) effect; Chinese students being slower than Dutch students. The paired-samples t-test showed that it takes longer to judge neutral bodies when they are in a fearful compared to a neutral scene ($t(37)=2.816$, $p=.008$, $d=.101$). See figure 6.

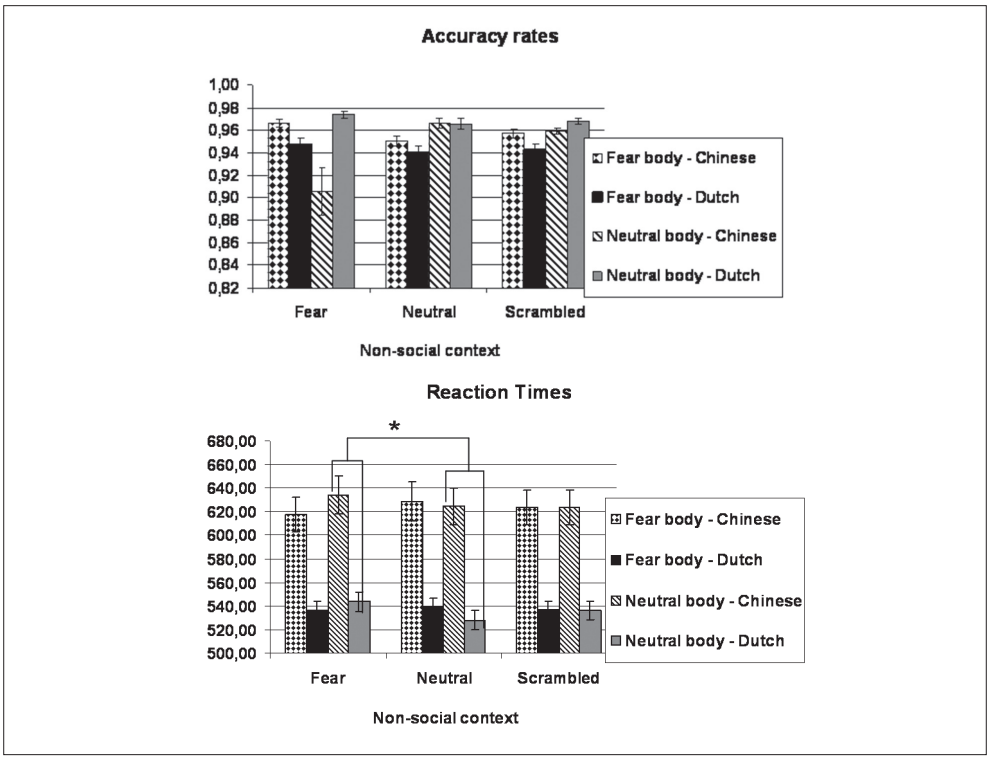

Figure 6. *Accuracy rates (showing a bodily emotion x group interaction) and reaction times (showing a body x scene interaction and a group effect) for bodily emotions in non-social context.*

Bodies in social contexts

Our expectation was that Chinese participants will be influenced more by the social scene than Dutch participants. Therefore, they should perform worse on incongruent social scenes. A 2 (group: Chinese/Dutch) x 2 (bodily emotion: fear/neutral) x 4 (scene: fear/happy/neutral/scrambled) repeated measures ANOVA with group as between-subjects factor was performed on again both the ACCs and the RTs. Again, independent- and paired-samples t-tests were performed to look into interaction effects. The ACC data showed a bodily emotion x scene ($F(3,105=3.727$, $p=.014$, $\eta p2=.096$), a scene ($F(3,105=4.153$, $p=.008$, $\eta p2=.106$) and a group effect ($F(3,105=13.823$, $p=.001$, $\eta p2=.283$) in that Chinese perform in general better than the Dutch. Pairwise comparisons show that fearful bodies when being in a fearful scene are better recognized than in an incongruent emotional scene (happy scene: $t(36)=2.982$, $p=.005$, $d=.649$; neutral scene: $t(36)=2.434$, $p=.020$, $d=.369$) and happy bodies are worse recognized when they are in a fearful scene than in a happy scene ($t(36)=2.065$, $p=.046$, $d=-.393$). The RT data only give a scene effect ($F(3,105=6.608$, $p=.000$, $\eta p2=.159$) which is caused by the scrambled ones for which participants are fastest. See figure 7.

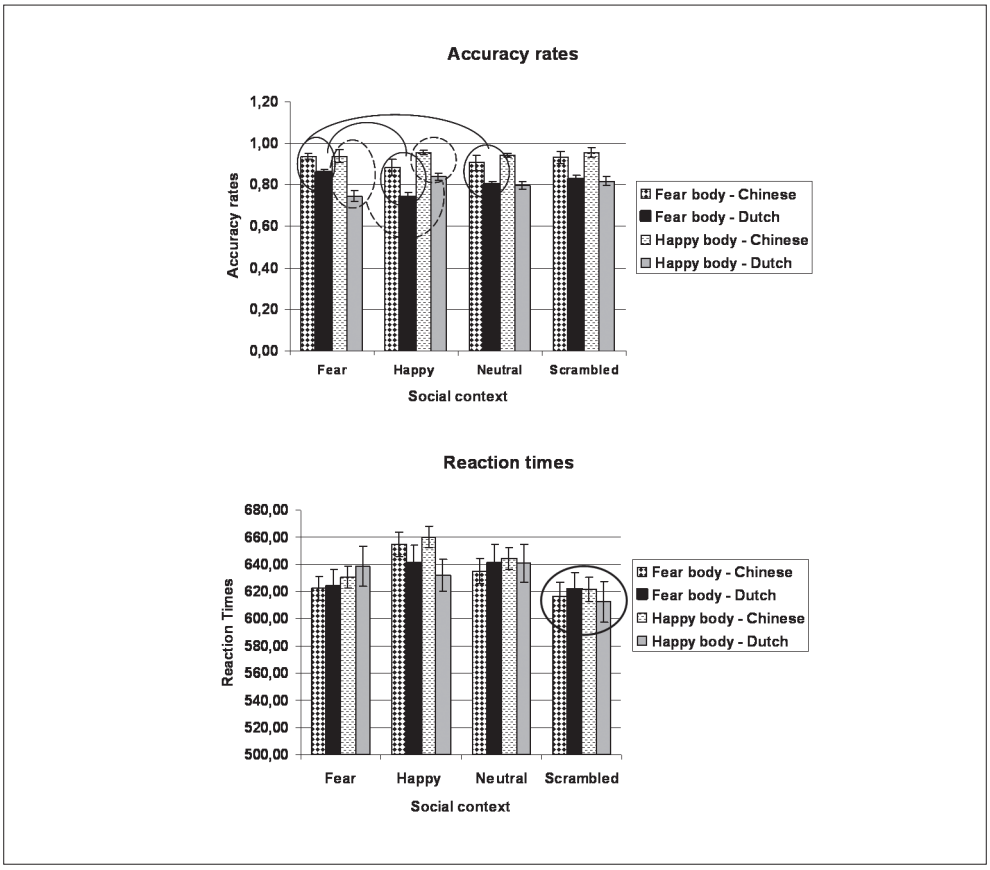

Figure 7. *Accuracy rates (showing a body x scene interaction, a scene effect and a group effect) and reaction times (showing a scene effect) for bodily emotions in social context.*

As a control, we also tested whether the participants could recognize the social scenes properly. For this, the scenes without target body were presented to the participants, whereby they had to indicate for each scene whether they thought it was neutral, fearful, happy or angry. On these data, a scene emotion (anger/fear/happy/neutral) x group (Chinese/Dutch) ANOVA was performed on accuracy. The ANOVA on the social scene recognition data showed an emotion effect ($F(3,150=12.899$, $p=.000$, $\eta p2=.205$). Happy social scenes were easiest for both groups. See figure 8.

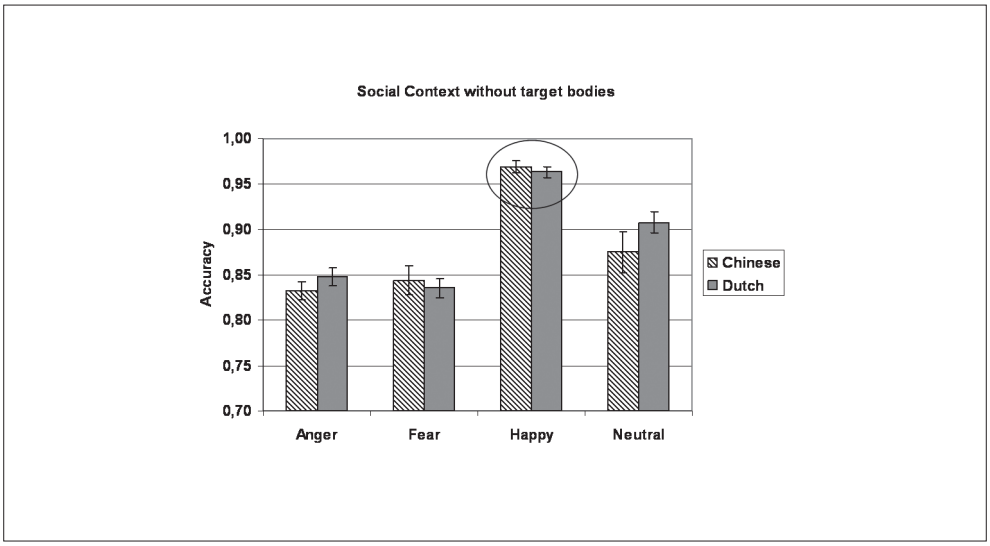

Figure 8. *Recognition rates for social context.*

Discussion

Our goal was to explore differences between Asian and Western individuals in the perception of facial and bodily emotions and the influence of a social context on the latter. Our main results are that the Chinese compared to Dutch participants have a recognition memory disadvantage for Caucasian faces which disappears when the faces show emotions; Chinese are better than Dutch in recognizing both Chinese and Caucasian individual faces and they respond to those faster than to bodies or shoes; to emotional Caucasian faces and bodies Chinese respond slower than Dutch; Chinese respond slower to (emotional) bodies in a non-social, but faster and better in a social context. We discuss the results by following the issues stated in the introduction.

Our first question concerned whether adding a facial expression influences recognition memory advantage for own race faces. This advantage has already been found present in black and white children although being in kindergarten together (Pezdek *et al.*, 2003). As expected, Chinese participants performed worse than Dutch on the neutral Caucasian faces recognition memory test. But this group difference disappeared once emotions are involved. Adding facial expressions improves memory performance for personal identity in other race faces. It is known that emotional faces capture attention (Vuilleumier & Schwartz, 2001) and lead to higher activation in the face-processing area in the brain (Vuilleumier *et al.*, 2001). This could lead to a better storage and hence better recollection of the faces.

Secondly, we replicate previous findings of an own-race bias in recognizing neutral faces. However, this is only the case for the Chinese participants who are more accurate on the Chinese face identity task, while the Dutch do not show this expected higher accuracy with Caucasian faces. When looking at the match-to-sample tasks in general, Chinese students are slower than the Dutch on all but the face identity tasks. And when directly comparing both face identity tasks for both groups, we find that Chinese students are on both more accurate than the Dutch group. These results could indicate that the Chinese are more focused on faces than Dutch. Maybe they are more experienced in looking carefully at faces since Chinese people are known to be more introvert. Chinese people might not always tell how they really feel, but an experienced observer could see this from subtle facial changes. Following this rationale, the emotions expressed by the Caucasian faces in the recognition memory test could be very intense for the Chinese subjects which was the reason why they remembered those faces better. Concerning our third issue, Chinese do indeed not perform differently in the emotion tasks, but they take more time to make a decision for all emotions except for happy faces. This facial expression is probably least ambiguous and most similar across cultures. Interestingly, sad seems to be the most prominently recognized bodily emotion as both groups were fastest in judging this emotion and were even all 100% correct.

Fourthly, we investigated the influence of context. Chinese participants were in general slower in judging the emotion of the target body in a non-social context than the Dutch. Since this difference was also found for the previous match-to-sample tasks it does not seem to be specific for the context. An incongruent stimulus consisting of a neutral body in a fearful social and non-social context slows down performance in both groups. Unexpectedly, Chinese students are not more affected by an incongruent social scene. The effect of an incongruent (happy or neutral) social scene on fearful target bodies and of a fearful social scene on happy target bodies is present in both groups as shown by the accuracy data. But overall, Chinese participants perform better than the Dutch which was not the case when the bodies were presented in a non-social context, or without context. An explanation for this could be that Chinese are in fact more influenced by the social scene but in a different way: because there are other people present they might feel a pressure to perform better. We know that such social cues can indeed have an influence on behavior (Bateson *et al.*, 2006), and because the Chinese students were brought up in a collectivistic society this can have a bigger effect on them. A possibility of why the incongruent social scenes did not distract could be because of the short stimulus duration of 100 ms. A previous study showed that Japanese participants who had to judge a target body within a social scene looked more at the other people in the scene but only after 1s (Masuda *et al.*, 2008). At least, it cannot be because the scenes were ambiguous, both groups recognized the emotion expressed by the people in the scene equally well and happy scenes were best recognized by both.

Conclusion

Our study yields interesting and novel insights into cultural differences between Chinese and Dutch participants. We find that emotions help overcome the recognition memory disadvantage for other-race faces. Additionally, Chinese participants seem to be more specialized for faces than Dutch participants; they are more accurate in recognizing both Chinese and Caucasian identities and they do this faster than identifying shoes or bodies. Concerning Caucasian emotions, Chinese participants need more time than Dutch to recognize the expression, whether it is expressed in the face or the body. They also need more time to recognize (emotional) bodies in a non-social context, but not in a social context. Here, Chinese actually are faster than Dutch. So although both groups are similarly influenced by an incongruent scene, the presence of a social scene has a positive effect on the Chinese participants in general. Our study shows the importance of broadening the scope of cross-cultural emotion research by focusing on bodily emotions and by considering the influence of contexts.

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Chapter 3

The influence of context on the processing of faces

"The behaviors related to the sympathetic division are summarized in the mnemonic called the four Fs: Fight, flight, fright, and sex"
~ from G. Bear, B.M. King & E.W. Minium:
Statistical Reasoning In Psychology And Education ~

Chapter based on:
Sinke, C.B.A., Van den Stock, J., Goebel, R. & de Gelder, B. The influence of context on the processing of faces. (in preparation)

Abstract

Humans rapidly recognize and understand facial expressions of others, as shown by numerous behavioral and neuroimaging studies. An important factor that may influence this recognition process is the context in which the face is perceived. Affective scenes have already shown to influence an ERP component (the N170) of facial expressions, indicating that the face is already at an early stage encoded differently in an affective context. We wanted to further explore these context effects using functional magnetic resonance imaging.

We tried to investigate the influence of either a congruent or incongruent scene on the neuronal processing of fearful and neutral faces. Fourteen participants were being scanned while they were shown photographs (248 trials) of either a fearful or a neutral face in a fearful, neutral or scrambled scene. To stay focused, they had to respond to an oddball, being an inverted stimulus. All bodies were replaced with the same black body-like shape for all identities and emotions, so no information could be extracted from this. The experiment consisted of four runs of 31 blocks. Eight stimuli were presented per block for 800 ms with an interval of 350ms. Also, a functional localizer for the perception of faces, bodies, houses and tools was used.

Our results show that activity in brain areas that are associated with perception of faces, occipital and fusiform face area, are not influenced by the emotional information conveyed by the scene. Parahippocampal place area and the area in parietal occipital sulcus related to processing perception of places showed less activation when the scenes were fearful as compared to neutral and were not influenced by the facial expressions. Only the place area in transverse occipital sulcus responded more when fearful faces were presented in the scene. Furthermore, place processing is decreased when a face is presented at the same time within the scene.

Introduction

In everyday life when we interact with or merely observe people, we tend to look foremost to their faces. However, we do not see faces in isolation. Whether we are aware of it or not, we also observe the body movements, the voice and surrounding events. Contextual information like these have much influence on how we perceive the face we look at. Probably most of us have had at least once the experience of passing someone on the street, recognizing the person, but you just cannot remember from what or where. It can be days later that you remember all of a sudden that this person works at the bakery you go to every week. Just because you observed the face in another surrounding than you normally do, you did not recognize him. This example clearly shows how important context is.

Context not only influences our recognition abilities of facial identity, it also influences our perception of facial expressions (Kret & de Gelder, 2010; Van den Stock *et al.*, 2008, 2009). Most emotion experimenters have used pictures of isolated faces although in real life, facial expressions can be ambiguous and it will only become clear to the observer what the expresser is feeling, once more information has become available to him.

Even a more abstract context can influence face perception. Surprised faces were said to show either positive or negative expressions by subjects when first given a positive or negative contextual sentence respectively (Kim *et al.*, 2004). This also led to differentiated brain activations; the amygdala (AMG) was activated only for negatively cued surprised faces.

Behavioral studies already showed contextual influence on face processing. In a study by Righart & de Gelder (2008b), subjects had to explicitly judge facial expressions of disgust, fear and happy which were presented in either a congruent or an incongruent scene. There was a congruency effect found in that subjects were faster to respond to emotional faces presented in an emotionally congruent scene. This was the case with short presentation times (200ms), indicating a rapid global perceptual scene analysis. This congruency effect remained present during an attention competing task. During this task, subjects had to indicate which character had been presented on the stimulus while at the same time also still having to explicitly judge the facial expression. This contextual processing facilitation had already been found to be present for objects, although this was more related to specific object-scene combinations that are commonly associated together in our life (Davenport & Potter, 2004).

This congruent contextual facilitation on facial expression perception had also been found before using EEG. The N170 is an ERP component on occipito-temporal sites of specific interest in face research. It has been found to be specifically involved in the processing of faces since the amplitude is bigger when participants see faces than when they see objects, and it is thought to reflect a late stage in the structural encoding of the visual stimulus (Bentin *et al.*, 1996). Whether, or how, the N170 is modulated by emotion, is still not clear. The many studies that have been performed on this topic have found conflicting results; *e.g.* Eimer *et al.* (2003) and Holmes *et al.* (2003) did not find an emotional modulation on this specific component (Eimer *et al.*, 2003; Holmes *et al.*, 2003) while for instance Williams *et al.* (2006) and Batty and Taylor (2003) did find a higher amplitude for fearful versus neutral faces (Batty & Taylor, 2003; Williams *et al.*, 2006). Holmes and colleagues (2003) did find an enhancement however, when faces were attended versus not attended (Holmes *et al.*, 2003).

Also, there has been looked for the behaviorally found context congruency effect in the N170. In one study, fearful and neutral faces were presented in a fearful or neutral context (Righart & de Gelder, 2006). The authors found that affective scenes influenced this component; the amplitude increased when faces were presented in fearful scenes and even more when also the faces were fearful. These results indicate

that the face is already at an early stage encoded differently when it is perceived in an affective context. Conversely, Hirai *et al.* (2008) did not find an interaction between contextual information and facial expression on the N170 (Hirai *et al.*, 2008).
The N170 is likely to originate from the fusiform gyrus (Horovitz *et al.*, 2004), where a region categorically involved in the processing of faces is located; the fusiform face area (FFA). Using functional magnetic resonance imaging (fMRI), we wanted to investigate whether a similar result as found on the N170 can be found in this region. To be more specific, the main question we tried to answer with this study was: has emotion from the scene influence on face processing? To answer this question we wanted to look not only in FFA, but also in occipital face area (OFA). Furthermore, if scene emotion could influence face processing, it might also work the other way. So as a subquestion we wanted to investigate: has emotion from the face influence on scene processing? For this question, we planned to look in regions known to be specifically involved in place processing: parahippocampal place area (PPA; Epstein & Kanwisher, 1998), retrosplenial cortex in parietal-occipito sulcus (POS; Bar & Aminoff, 2003) and thirdly an area located in the transverse occipital sulcus (TOS; Hasson *et al.*, 2003). Finally, we also were interested in how the AMG would respond to these specific stimuli, since it known to be responsive to fearful faces and it was also found for the perception of affective scenes (Hariri *et al.*, 2002). The contexts we used were natural, non-social scenes being neutral or fearful. The faces portrayed in it could be emotionally congruent or incongruent with the scene.
This realistic pairing of face and scene has not been done before in an fMRI study as far as we know. One study paired a context with two face stimuli underneath for which subjects had to match the face with the emotion congruent to the scene (Sommer *et al.*, 2008). In another study a context was shown first for several seconds, followed by a jittered fixation interval, to be followed then by a shortly presented face stimulus that needed to be emotionally judged (Mobbs *et al.*, 2006). This way of presenting gives rise to expectations, while we were interested here in basic perception.

Methods

■ Participants

Fifteen healthy volunteers (six male; 26.2 ± 5.9 years; all right-handed) participated in this experiment after providing a written informed consent. All participants had normal or corrected-to-normal vision. The study was performed in accordance to the *Declaration of Helsinki* and was approved by the local medical ethical committee. One subject was excluded from analysis due to excessive head movement.

■ Materials

Pictures from scenes were taken from the internet. The scenes contained a house, a car or a landscape being either neutral or fearful (*e.g.* a house on fire, a crashed car or a tornado). No people or animals were present in the scenes. The pictures were resized to 768 x 576 and were validated on emotional intensity in a pilot study. They were presented for 4000ms with a 4000ms interval in a pilot study. Participants were instructed to categorize as accurately and as quickly as possible the pictures according to the emotion they induced in the observer. 24 scenes (half neutral, half fearful) were selected for the present experiment (all recognized correctly above 70%). Additionally, scrambled versions were created of every scene, by dividing it in 10 000 (100 x 100) squares and randomly rearranging the squares.

24 different faces (half male; half neutral, half fearful) were taken from the Karolinska Directed Emotional Face database (Lundqvist *et al.*, 1998) and placed in the middle of the scenes, leading to nine different stimulus conditions (see Fig. 1). In order to avoid the unreal appearance of floating faces, and because we only wanted to look at facial expressions, a black body-like shape was placed underneath each face. This shape was the same for all identities and emotions, so no information could be extracted from this. Besides having a neutral (Nf) or a fearful face (Ff) appearing in a neutral (Ns) or a fearful scene (Fs), a face could also appear on scrambled scene background (Xs), and instead of a face a triangle (Xf) could appear on top of the three background types.

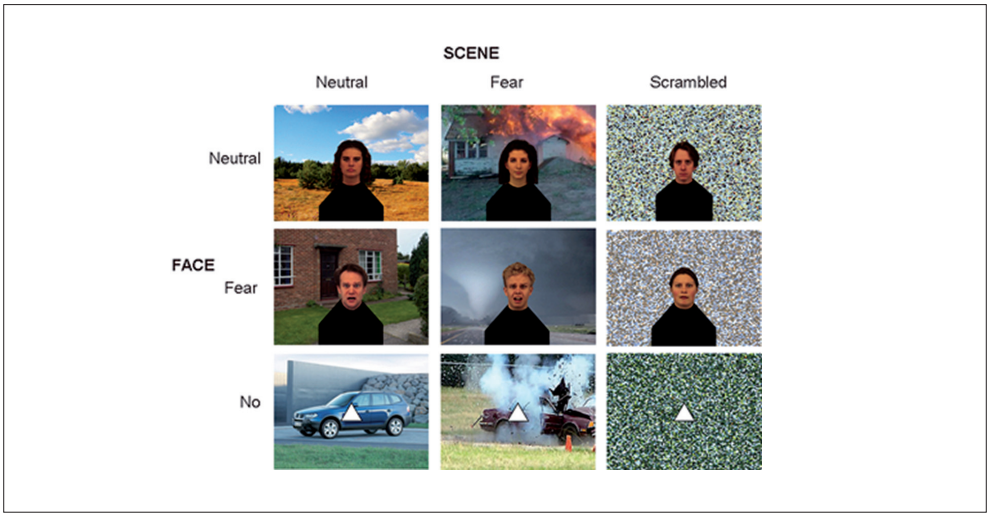

Figure 1. *3x3 factorial design. Neutral and fearful faces were overlaid centrally on a neutral or fearful scene. As controls, scrambled scenes and triangles instead of faces were used.*

■ Design and procedure

A blocked design was used to maximize blood oxygenation level dependent (BOLD) effects. In one stimulus block, eight stimuli were presented for 800ms with an interstimulus interval (only fixation cross) of 325ms. Every session comprised 4 runs of 31 stimulus blocks and 32 fixation blocks, with an anatomical scan in the middle. At the end, a localizer run for the perception of faces, bodies, houses and tools was given. For the experimental runs, subjects were instructed to look at the middle of the screen and pay careful attention whether a picture was upside down, in which case they had to press a button. This oddball appeared four times per run. The blocks in which an oddball appeared, were discarded from analysis. During the localizer run, subjects had to do a one-back task to be sure they were attentive to the stimuli. Again, blocks requiring a button response were discarded from analysis.

Stimuli were presented with Presentation software (Neurobehavioral Systems, Inc, version 11.0). A total 864 trials (without the oddball blocks) were presented; 96 trials (12 blocks) per condition. All stimuli were generated by a PC and projected onto a frosted screen located at the end of the scanner bore (at the side of the participants' head) with a liquid crystal display (LCD) projector (PLC-XT11-16, Sanyo North America Corporation, San Diego, USA). The participants viewed the stimuli via a mirror mounted to the head coil at an angle of ± 45°.

Right after the scanning session, participants had to perform a behavioral task to test their recognition of the faces. For this, exactly the same stimuli were used as in the fMRI experiment, only the stimuli without faces were not used. Participants' task was to indicate for each picture whether the face was fearful or neutral by a button press as fast as possible. All stimuli were presented twice for 800ms.

■ fMRI data acquisition

The MRI unit used was a commercial head scanner with a magnetic field strength of 3T (Siemens Allegra, AG, Erlangen, Germany) provided with a standard quadrature birdcage head coil. Foam padding placed around the head was used to minimize movement and the participants were provided with ear plugs to reduce the scanner noise.

In each session, a three-dimensional (3D) T1-weighted data set named Alzheimer's Disease Neuroimaging Initiative (ADNI) encompassing the whole brain was acquired (scan parameters: repetition time (TR) = 2250ms, echo time (TE) = 2.4ms, flip angle (FA) = 9°, field of view (FOV) = 256 × 256mm^2, matrix size = 256 × 256, number of slices = 192, slice thickness = 1mm, no gap, total scan time = 8m and 5s).

The scan parameters of the functional sequence used were: TR = 2250ms, TE = 25ms, FA = 90°, FOV = 224 × 224mm^2, 42 slices, slice order = descending-interleaved, slice thickness = 2.5mm (no gap), number of volumes = 348 (total scan time = 13m 3s).

For the localizer scan different parameters were used to achieve a higher spatial resolution: TR= 2000ms; TE= 30ms; FA= 90°; FOV= 256 x 256mm^2; 28 slices of 2mm (no gap), slice order = descending-interleaved. The run comprised 20 blocks of 12s/ 6TR, interleaved with fixation blocks of 14s/ 7TR. The total duration of the localizer was 8m and 54s, being 267 functional volumes.

■ Behavioral data analysis

Using SPSS (version 15.0 for Windows), a repeated measures univariate analysis of variance (ANOVA) was performed with the two factors face and scene and respectively two and three levels (neutral, fearful plus for the latter scrambled) to test whether there was a difference in performance between recognition of neutral and fearful faces in different scenes.

■ FMRI data analysis

For the fMRI data analysis BrainVoyager QX (version 1.10.4 Brain Innovation, Maastricht, the Netherlands) was used. A number of preprocessing steps were performed on the functional data. These included incremental linear trend removal to eliminate scanner-related signal drifts; temporal high-pass filtering to remove temporal frequencies lower than 3 cycles per run; and a rigid body algorithm which rotates and translates each functional volume in 3D space in order to correct for small head movements in between scans. For the group ANOVA on the volume and the surface, the data was spatially smoothed with a 4mm Gaussian kernel. To enable the comparison between participants, all anatomical as well as functional volumes were spatially normalized into Talairach space. The first two scans per run were excluded from the analysis to permit T1 equilibration effects. The 3D T1-weighted scans were used to overlay the statistical maps on for anatomical orientation.

At single-subject level, several regions-of-interest (ROIs) were localized in each individual brain. For the face areas – OFA and FFA –, responses to the faces were contrasted with those of houses and tools. FFA ROIs were chosen with at least false discovery rate (FDR) (q)<.1 and only 1 subject at p<.02, to be able to get cluster sizes of 50-200 voxels. The place areas – PPA, RHC and TOS – were defined by contrasting houses *versus* tools, faces and bodies. Those areas were chosen with relatively liberal uncorrected criterion (minimum p < .05, 50-200 voxels). Beta-values from the ROIs were extracted from BrainVoyager into SPSS (Version 15.0) in order to perform a random effects ANOVA to look for main effects of face and scene and for interaction effects. Also, paired-samples t-tests were performed to further look at the interaction effects.

Furthermore, fixed-effects whole brain ANOVAs were performed using a regression model consisting of the nine predictors corresponding to the particular experimental conditions (neutral, fearful or no faces in a neutral, fearful or scrambled scene) plus

one for the oddball blocks. The predictor time courses used were generated on the basis of a linear model of the relation between neural activation and hemodynamic response.

At group level, a single subject ROI-based group ANOVA with two within-participants factors (face, scene) with three levels (neutral, fearful, scramble/triangle) had been performed, using a threshold of $p < .05$. Secondly, a whole brain random effects ANOVA with the same factors was performed to look for interaction effects. The resulting volume maps per contrast were subjected to a cluster-level statistical threshold analysis in order to correct for multiple comparisons (Forman *et al.*, 1995; Goebel *et al.*, 2006). Only the group results are reported. A separate comparative analysis looking specifically to the brain response to fearful faces in fearful scenes *vs.* neutral faces in neutral scenes has been discussed separately (Sinke *et al.*, submitted).

Results

■ Behavioral results

Participants were better in recognizing the neutral than the fearful faces as shown by repeated measures ANOVA ($F(1,13) = 16.318$, $p = .001$, $\eta p2 = .56$). There was also a scene effect for accuracy ($F(1,12) = 4.006$, $p = .046$, $\eta p2 = .40$); participants were better in recognizing faces when they had appeared on a scrambled than a neutral background ($p < .046$). For the reaction times, there was only a trend for a scene effect ($F(1,12) = 2.255$, $p = .179$, $\eta p2 = .27$), revealing that participants were slightly faster in recognizing faces in a neutral than in a fearful scene ($p < .139$). See figure 2.

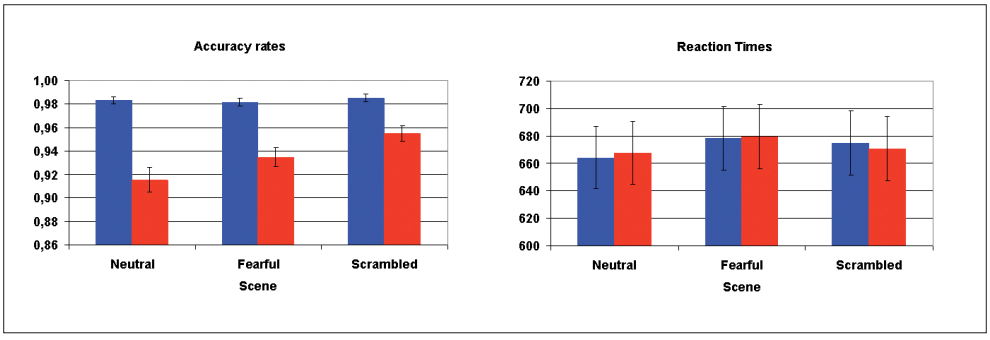

Figure 2. *Accuracy rates showed a main effect of face (neutral (blue bars) > fearful (red bars)) and scene (scrambled > neutral). Reaction times only showed a trend for main effect of scene (neutral < fearful).*

■ FMRI results

ROI analysis

It was possible to locate in almost every subject the ROIs we were interested in. Table 1 shows the average Talairach coordinates per ROI. All interactions effects are put in Table 2 and Figure 3-5 show the results of the face and place areas and AMG.

Table 1. *Average Talairach coordinates for all regions-of-interest (ROI).*

ROI	Hemisphere	x *(SD)*	y	z
OFA	L	-37 *(5.6)*	-64 *(7.1)*	-9 *(3.5)*
OFA	R	38 *(3.5)*	-66 *(8.8)*	-7 *(5.6)*
FFA	L	-38 *(4.4)*	-44 *(9.5)*	-14 *(4.3)*
FFA	R	38 *(3.2)*	-44 *(7.1)*	-13 *(3.6)*
PPA	L	-25 *(4.3)*	-44 *(6.2)*	-4 *(2.4)*
PPA	R	25 *(4.0)*	-44 *(4.7)*	-5 *(2.5)*
POS	L	-15 *(5.0)*	-55 *(4.8)*	15 *(4.9)*
POS	R	15 *(4.6)*	-53 *(4.6)*	17 *(2.8)*
TOS	L	-28 *(3.8)*	-82 *(4.1)*	23 *(6.7)*
TOS	R	30 *(5.6)*	-81 *(4.6)*	22 *(6.8)*

Left OFA was located in only 9 subjects, right OFA in 12, left POS in 10, right POS in 12, and left TOS in 13 subjects.

Table 2. *Interactions found in regions-of-interest (ROI).*

ROI	Hemisphere	contrast	*df*	*t*	*d*	*p*
OFA	R	FfFs > XfFs	11	4.690	1.05	.001
		FfXs > NfXs	11	2.476	.29	.031
		XfFs > XfNs	11	3.883	.31	.003
		NfNs > NfFs	11	1.706	.21	.116
FFA	L	FfFs > NfNs	13	3.008	.27	.001
		FfNs > NfNs	13	4.885	.36	.000
		FfFs > XfFs	13	6.586	1.21	.001
		FfXs > NfXs	13	1.989	.23	.068
FFA	R	FfFs > XfFs	13	5.072	1.73	.000
		XfFf > XfNs	13	3.638	.49	.003
		FfNs > NfNs	13	1.577	.17	.139
		FfFs > NfFs	13	1.710	.21	.111
PPA	L	XfFs > FfFs	13	1.931	.72	.000
		NfNs > FfFs	13	3.578	.34	.003
		NfNs >NfFs	13	2.520	.35	.026
		FfNs > FfFs	13	2.303	.37	.038
PPA	R	XfFs > FfFs	13	4.924	.97	.000
		NfNs >NfFs	13	2.687	.37	.019
		NfXs > FfXs	13	1.549	.14	.145
		FfFs > NfFs	13	2.121	.24	.054
POS	L	XfFs > FfFs	9	3.296	.65	.009
		NfNs >NfFs	9	3.429	.64	.008
		FfNs > FfFs	9	2.818	.57	.020
		NfNs > FfFs	9	1.990	.38	.078
		FfNs > NfNs	9	1.625	.20	.139
POS	R	XfFs > FfFs	11	2.540	.47	.027
		NfNs > FfFs	11	2.543	.28	.027
		NfNs >NfFs	11	2.418	.45	.034
		FfNs > FfFs	11	2.009	.34	.070
TOS	L	XfFs > FfFs	12	6.276	1.05	.000
		FfFs > NfFs	12	2.217	.22	.047
		NfXs > FfXs	12	1.587	.20	.139
		FfFs > NfNs	12	1.714	.23	.112
TOS	R	XfFs > FfFs	13	3.695	.56	.003
		FfFs > NfFs	13	2.482	.19	.028

In left PPA there was a trend for an interaction (p<.109), paired-samples t-tests results are here only mentioned for your interest.

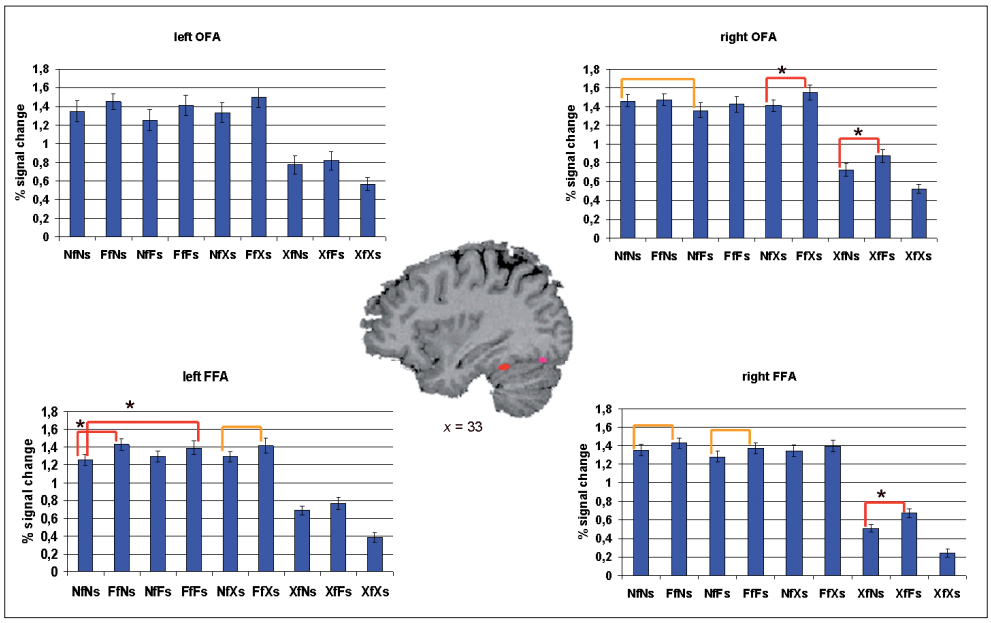

Figure 3. *Region-of-interest-based group analyses in the face areas. Occipital face area (OFA; pink cluster) in left hemisphere only showed a main effect of face (fearful > neutral > triangle). Right OFA and bilateral fusiform face area (red cluster) showed an interaction between emotion from face and scene. (Red lines marked with an asterisk (*) indicate significance at the level of p<.05. Yellow lines indicate a trend for significance.)*

Left OFA showed a face effect ($F(2,7) = 31.350$, $p = .000$, $\eta_{p2} = .90$): there was more activation for a fearful than a neutral face ($p<.002$) than a triangle ($p<.000$). Right OFA showed an interaction ($F(4,8) = 9.140$, $p = .004$, $\eta_{p2} = .82$) and a main effect for face ($F(2,10) = 23.443$, $p<.000$, $\eta_{p2} = .82$).

An interaction effect ($F(4,10) = 9.439$, $p = .002$, $\eta_{p2} = .79$) together with a face ($F(2,12) = 27.003$, $p = .000$, $\eta_{p2} = .82$) and scene ($F(2,12) = 4.180$, $p = .042$, $\eta_{p2} = .41$) effect was found in left FFA. Right FFA also shows an interaction ($F(4,10) = 11.258$, $p = .001$, $\eta_{p2} = .82$), a face ($F(2,12) = 26.115$, $p = .000$, $\eta_{p2} = .81$) and a scene ($F(2,12) = 5.481$, $p = .002$, $\eta_{p2} = .48$) effect.

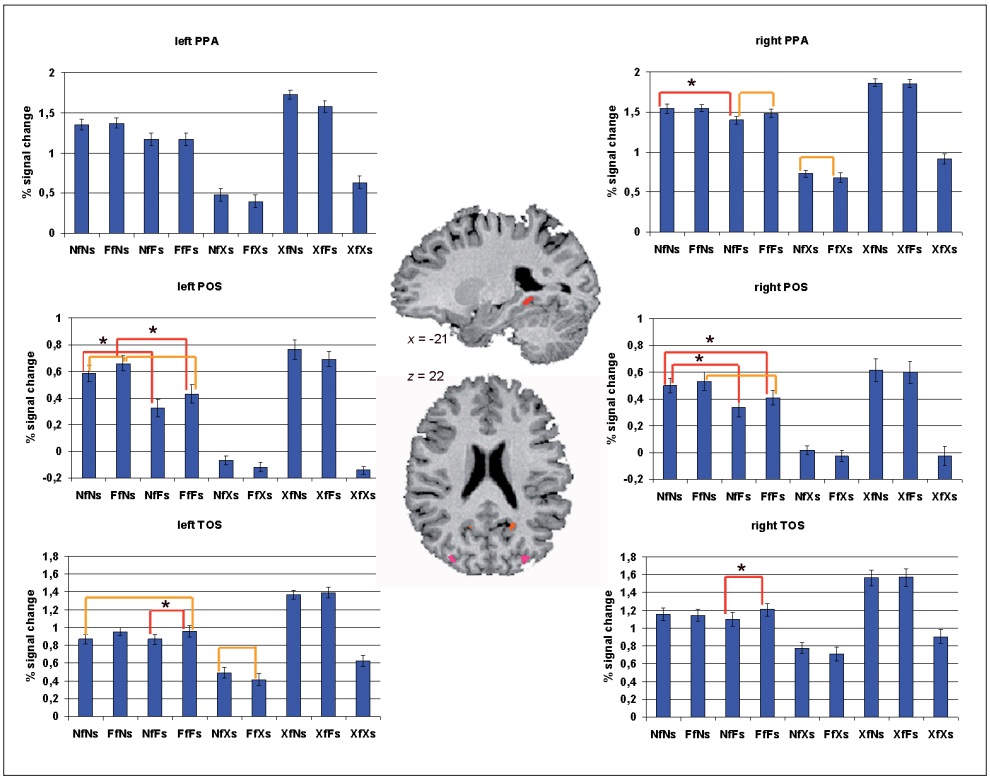

Figure 4. *Region-of-interest-based group analyses in the place areas. Parahippocampal place area (PPA; red cluster) in left hemisphere showed a main effect of scene (neutral > fearful > scrambled) and face (triangle > neutral & fearful). Right PPA, parietal occipital sulcus (orange cluster) and transverse occipital sulcus (pink cluster) showed an interaction. (Red lines marked with an asterisk (*) indicate significance at the level of p<.05. Yellow lines indicate a trend for significance.)*

Left PPA showed a main effect of scene ($F(2,12) = 75.956$, $p = .000$, $\eta_{p2} = .93$) and a main effect of face ($F(2,12) = 22.001$, $p = .000$, $\eta_{p2} = .79$). Neutral scenes give rise to more activation in this area than fearful scenes independent of face ($p<.012$) and both got activated more than scrambled scenes (both $p<.000$). Scenes without faces gave rise to more activation than scenes with faces, independent of emotion (for neutral as well as fearful faces $p<.000$). Since there was a trend for an interaction ($F(4,10) = 2.508$, $p = .109$, $\eta_{p2} = .50$), we looked exploratory into the t-tests. Right PPA showed an interaction between face and scene ($F(4,10) = 4.529$, $p = .024$, $\eta_{p2} = .64$). Furthermore, there was a scene ($F(2,12) = 73.365$, $p<.000$, $\eta_{p2} = .92$) and a face ($F(2,12) = 23.885$, $p<.000$, $\eta_{p2} = .80$) effect.

Left POS showed an interaction ($F(4,6) = 7.825$, $p<.015$, $\eta_{p2} = .84$) plus a main effect for both scene ($F(2,8) = 29.438$, $p<.000$, $\eta_{p2} = .88$) and face ($F(2,8) = 10.331$, $p<.006$, $\eta_{p2} = .72$). Right POS also showed an interaction effect ($F(4,8) = 4.460$, $p<.035$, $\eta_{p2} = .69$) and a main effect of scene ($F(2,10) = 14.531$, $p < .001$, $\eta_{p2} = .74$).
TOS showed an interaction (left: $F(4,9)= 8.078$, $p<.005$, $\eta_{p2} = .78$; right: $F(4,10)= 4.840$, $p<.020$ $\eta_{p2} = .66$), a scene (left: $F(2,11)= 73.126$, $p<.000$ $\eta_{p2} = .93$; right: $F(2,12)= 16.571$, $p<.000$ $\eta_{p2} = .73$) and a face (left: $F(2,11)= 34.931$, $p<.000$ $\eta_{p2} = .86$; right: $F(2,12)= 9.594$, $p<.003$ $\eta_{p2} = .62$) effect.

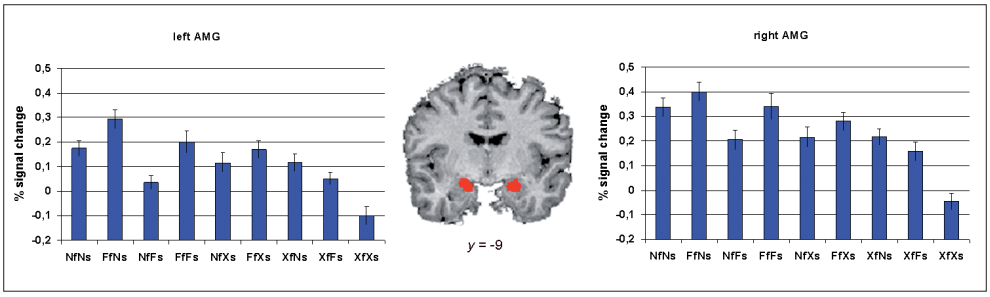

Figure 5. *Region-of-interest-based group analysis in the amygdala. Both sides showed a main effect of face (fearful > neutral > triangle) and scene (left: neutral > fearful & scrambled; right: neutral & fearful > scrambled).*

Left AMG showed a main effect of scene ($F(2,11= 8.132$, $p<.007$, $\eta_{p2} = .60$), being more active for neutral than fearful ($p<.025$) and scrambled ($p<.001$) ones, and a main effect of face ($F(2,11)= 4.715$, $p<.033$, $\eta_{p2} = .46$), being more active for fearful than neutral ones ($p<.002$) and than for no face stimuli ($p<.001$). Right AMG also showed a main effect of scene ($F(2,11= 6.535$, $p<.013$, $\eta_{p2} = .54$) and face ($F(2,11)= 7.982$, $p<.007$, $\eta_{p2} = .59$). But here, the neutral scenes were only by trend different from the fearful ones ($p<.102$) and fearful from scrambled ones ($p<.104$). It was clear that neutral differed from scrambled ($p<.003$). Concerning the faces, fearful ones were more active than the neutral ones ($p<.010$) and the triangles ($p<.007$), neutral was only marginally higher than no faces ($p<.071$). See Figure 5.

Whole brain analysis

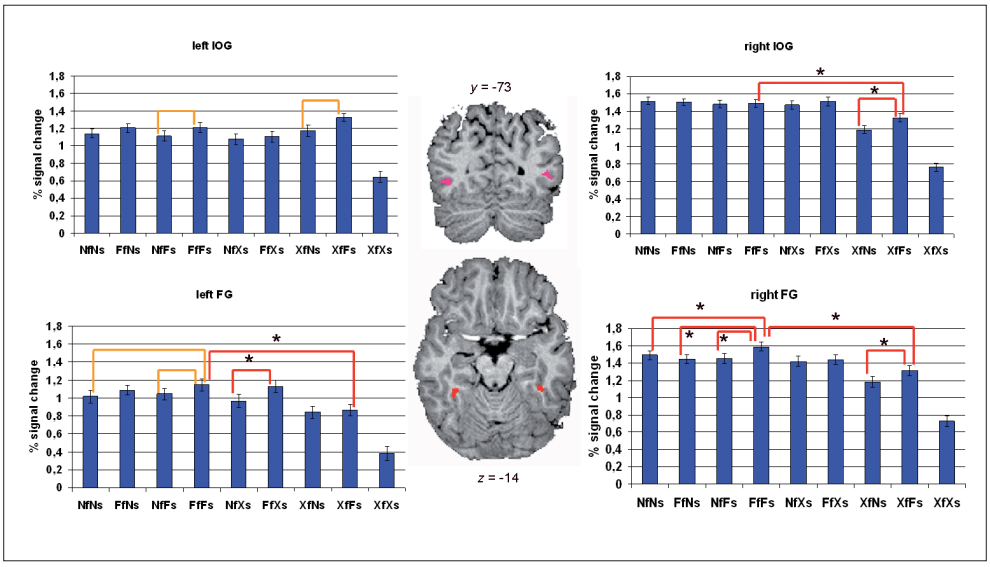

Figure 6. *Interaction in inferior occipital (IOG) and fusiform gyrus (FG) as found with whole brain analysis. (Red lines marked with an asterisk (*) indicate significance at the level of p<.05. Yellow lines indicate a trend for significance.)*

Regions showing an interaction between face and scene emotion. The whole-brain analysis showed an interaction between face and scene in the whole ventral object processing stream at FDR(q)<.05 bilaterally which seemed to be mainly due to a large decline in activation for scrambled scenes without face.

We decreased the threshold to get separate clusters (of 50-450 voxels). These were bilateral IOG (at Bonferroni correction p<.05), FG (left at FDR(q)<.01, right at Bonferroni (p)<.05), SOG (left at FDR(q)<.05, right at FDR(q)<.1) and an area in right collateral sulcus (at FDR(q)<.1). Table 3 shows the direction of the interactions, Figure 6 the results of IOG and FG.

Table 3. *Interactions found with the whole brain analysis.*

ROI	Hemisphere	contrast	*df*	*t*	*d*	*p*
Inferior occipital gyrus	L	FfFs > NfFs	13	1.723	.22	.109
		XfFs > XfNs	13	2.003	.38	.063
Inferior occipital gyrus	R	FfFs > XfFs	13	2.292	.49	.039
		XfFf > XfNs	13	2.334	.40	.036
Fusiform Gyrus	L	FfFs > XfFs	13	2.532	.58	.025
		FfXs > NfXs	13	2.684	.31	.019
		FfFs > NfNs	13	1.922	.25	.077
		FfFs > NfFs	13	1.716	.21	.110
Fusiform Gyrus	R	FfFs > NfNs	13	2.220	.26	.046
		FfFs > NfFs	13	2.822	.35	.014
		FfFs > FfNs	13	2.623	.38	.021
		FfFs > XfFs	13	2.569	.68	.023
		XfFs > XfNs	13	3.254	.29	.006
Superior occipital gyrus	L	XfFs > FfFs	13	5.827	.90	.000
		FfNs > NfNs	13	2.733	.30	.017
		XfFs > XfNs	13	2.084	.13	.057
Superior occipital gyrus	R	XfFs > FfFs	13	3.972	.37	.002
		FfNs > NfNs	13	1.775	.09	.099
Collateral sulcus	R	XfFs > FfFs	13	2.016	.34	.065
		NfXs > FfXs	13	1.778	.16	.099
		FfFs > NfFs	13	1.580	.31	.138

Discussion

Our main question for this study was whether emotional scenes influence face processing, namely we expected to find more activation in traditional face processing areas for both neutral and fearful faces when being presented in a fearful *vs.* a neutral context. However, we did not find this in our ROIs. OFA and right FFA are emotionally modulated by the face in accord with previous literature (Vuilleumier *et al.*, 2001). Furthermore, FFA seems to be affected by the scene, by showing also a main effect for threatening *vs*. neutral scenes, even though the region does respond less to the scenes when there are no faces. Just contrary to our expectations, in right OFA there is a trend for neutral faces to lead to less activation when presented in a fearful context. So in this region less face processing seems to be going on which could be because the fearful scene captures the attention. When there is also a fearful face, there are two

threatening sources that compete for attention. In this case, the fear from the scene does not heighten (emotional) face processing.

Even though the expected effect was not found in the conventional face areas, the whole brain analysis revealed an interaction between emotion from the scene and the face in IOG and FG. On the left side, there was only a trend for more activation for a fearful face in a fearful than neutral scene. In right FG this effect was very clear though, a fearful face in a fearful scene gave rise to more activation than any other face-scene combination. This is consistent with the effect found on the N170, where the amplitude increases for fearful faces in fearful *vs.* neutral scenes (Righart & de Gelder, 2006). However, the additive effect of a fearful scene on a face only was the case here when the face was fearful while the N170 also showed an enhanced amplitude for neutral faces in fearful *vs.* neutral scenes. Of course, this is measured with a totally different method which can not be directly compared. The N170 shows a very early, quick process that can probably not be picked up by fMRI. This effect on the N170 is not because of simple incongruency because another study by Righart & de Gelder (2008a) again found this enlarged N170 effect for faces in a fearful scene but not with an incongruent happy scene (Righart & de Gelder, 2008a).

The fact that different interaction results are found in the whole brain-found interaction regions and the individually localized face areas implies that different parts of face processing takes place within multiple areas in the FG than just in the conventional face areas. This can also be seen by the activation of the whole ventral object processing stream. Some of the individually localized areas overlap with the area in FG found with the whole brain analysis for all subjects together, while others do not. Also, the response to the faces in the face areas is already quite high, so there could be a ceiling effect which inhibits the modulation to be able to take place. With improved imaging methods, this might be shown in the future.

Our subquestion concerning the place areas, that they would respond more to threatening scenes than neutral ones was also not found. In all areas it was found that there was a higher response for threatening scenes without faces than when including a fearful face. Apparently, the emotion from the face takes away scene processing, even though that one is fearful as well. Maybe faces receive priority in the competition for processing. This is supported by the fact that all three place areas showed more activation when no face was presented, and the face areas do not show less activation when a scene is included. On the other hand, this could also be the case because the face is presented in the middle of the picture/screen. However, 800ms is long enough to also focus on the surrounding, as behavioral data have shown that the scene is very quickly – within 200ms – integrated (Righart & de Gelder, 2008b).

POS and left PPA showed less activation for fearful than neutral scenes. This implies that emotion processing does not take place here, but actually hinders scene processing here. Whether the face is threatening or not does not have an effect on scene processing in these areas. TOS did not show differential activation for neutral

and fearful scenes. But there was more activation for a fearful scene when a fearful instead of a neutral face was presented in it. So here, emotion from the face does have an influence. Apparently, this area processes scenes differentially than the other two place areas.

The AMG did not show an interaction effect. It was in general more responsive to fearful than neutral faces as could be expected from previous literature. The left and right side responded differently to the scenes though. While right AMG did not show a distinction between fearful and neutral scenes, left AMG responded less to fearful than neutral ones. This is quite unexpected. Threatening scenes have found before to actually increase AMG activation. Hariri and colleagues (2003) found it responding to fearful scenes, although less than to fearful faces (Hariri *et al.*, 2003). Also, they found a hemispheric difference; the right side responded more to faces and the left side more to scenes. Here, we found only a higher percent signal change in general in right than left AMG. Additionally, a previous study whereby emotional contexts were followed by shortly presented faces showed to increase AMG response (Mobbs *et al.*, 2006).

The behavioral results show that subjects respond faster and better for neutral than fearful faces. No interaction with the emotion from the scenes was found, which might be due to the pretty long stimulus duration of 800ms which gives enough time to reflect on the whole scene, instead of observing everything instantly. Previous research that did find an effect of scene emotion on facial expression judgments used shorter stimulus durations of 200ms (Righart & de Gelder, 2008a).

Conclusion

Faces in fearful scenes in general are not differently processed. Only when the face is fearful, the processing is modulated by a threatening scene. The place areas do not seem to process emotion; there is actually less response here when the scene is fearful as compared to neutral. Activity in TOS, but not in PPA and POS, is modulated by the emotion from the face. Face processing seems to have priority over place processing since the place areas respond less to the scenes once a face is presented in it.

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Chapter 4

Fearful scenes trigger activation in extrastriate body area

"Action readiness change is the major feature of emotion; … the defining feature."
~ N.H. Frijda, The Emotions (1986, pg. 469) ~

Based on the submitted article:
Sinke, C.B.A., Van den Stock, J., Goebel, R. & de Gelder, B. The constructive nature of affective vision: seeing fearful scenes activates extrastriate body area

Abstract

Scenes representing highly emotional events are normally associated with characteristic behavior. It is part of basic emotions like fear or anger that they prepare the brain to act adaptively. Here, we provide neuroimaging evidence that the extrastriate body area (EBA) is highly responsive to viewing isolated faces in familiar emotional scenes. The specific association of EBA activity with threatening scenes gives rise to speculation about the role of emotional contextual cues and might indicate that the brain reacts proactively to the meaning of the scene.

Introduction

There is increasing evidence that the perceptual system is constructive and actively fills in and anticipates information rather than that it passively represents given stimuli [Esterman & Yantis, 2010; Goebel *et al.*, 1998]. Typical contexts can trigger the representation of an object which is not physically present in the scene the observer is watching (Bar & Ullman, 1996). For example, when viewing a scene in which the occurrence of faces is highly probable, the face representations in the brain are active even when no faces are shown in the scenes (Cox *et al.* 2004). These constructive abilities of perception appear to be especially useful in case of affective stimuli (Sabatinelli *et al.*, 2001). Indeed, since Darwin it has been argued that preparing the organism for future adaptive action is at the core of emotion states. In line with this, visual scenes representing highly emotional events are associated in our mind with the appropriate actions (Frijda, 2010). For instance, when viewing an image of an explosion or of a house on fire, it is part of our understanding of the affective significance of the image to complete the picture by imagining people running away. In the present paper we discuss this.

The results presented here are part of a larger study, the one presented in Chapter 3 of this thesis. They are discussed separately because it seemed as if the brain spontaneously activated a representation of bodies even when no bodies were present in the scene. The complete experiment was designed to study the influence of context on the processing of faces. More specifically, we wanted to know whether the fearful emotion from the scene would increase activation in face processing areas, using functional magnetic resonance imaging (fMRI). In a previous study, it did heighten the amplitude of the N170, an event-related potential related to the processing of faces, for both neutral and fearful faces in a fearful vs. a neutral context (Righart & de Gelder, 2006). For this study, we used neutral and fearful scene stimuli with a neutral or fearful facial expression overlaid on them, as well as controls for the scenes and faces separately.

For the subset of findings discussed in the present paper, we compared the scene-only and the scenes-faces conditions to rule out that the putative activity in extrastriate body area (EBA) was not simply due to stimulus completion. Furthermore, in all the face present conditions the same geometrical figure was positioned below the face. In line with emotional action readiness theory we conjectured that this body related brain activity reflects the specific valence of the scene. This theory states that all kinds of emotions lead to different states of action tendencies in a person, either to approach or move away from the emotional source (Frijda, 1988). Following up on this theory, activation for concealed bodies should be highest when subjects view a fear evoking scene which would indicate that beyond filling in the missing body representation, the brain anticipates the bodily action appropriate for the scene. Bodies are known to specifically activate EBA (Downing *et al.*, 2001) and fusiform body area (FBA (Peelen & Downing, 2005)), which are modulated by emotion (Grèzes *et al.*, 2007; Sinke *et al.*, 2010). In contrast to FBA, EBA is spatially separated from the fusiform face area (FFA) so there can be no confusion about its possible activation related to the non-present bodies.

Materials and methods

■ Participants

Fifteen healthy volunteers (six male; 26.2 ± 5.9 years; all right-handed) participated in this experiment, but one subject was excluded from analysis due to excessive head movement. The study was performed in accordance to the *Declaration of Helsinki* and was approved by the Ethics Committee of the faculty of Psychology and Neuroscience (ECP Maastricht, the Netherlands). All participants gave written informed consent.

■ Design

We created nine stimulus conditions leading to a 3x3 design (see Fig. 1 of Chapter 3). A neutral (Nf) or a fearful face (Ff) was placed in the middle of a neutral (Ns) or a fearful scene (Fs). As control conditions, a face could also appear on scrambled scene background (Xs), and instead of a face a triangle (Xf) could appear on top of the three background types. Underneath all faces in all conditions, the same body-like shape was placed so no specific information could be extracted from those. 24 different scenes (half neutral, half fearful) and 24 different faces (half male; half neutral, half fearful) from the Karolinska Directed Emotional Face database (Lundqvist *et al.*, 1998) were used. Each identity was used in all conditions.

A blocked functional magnetic resonance imaging (fMRI) design was used. In one stimulus block of 9s, eight stimuli were presented for 800ms with an inter stimulus interval (only fixation cross) of 325ms. Subjects had to press a button whenever an

oddball (an inverted picture) appeared. The aim of this task was to keep participant's attention on the screen. Blocks including an inverted picture were discarded from analysis. Fixation blocks separated stimulus blocks with a duration of 15.75s. In total, 108 stimulus blocks (excluding sixteen interleaved oddball blocks) were presented in four runs.

An independent localizer run was used to locate face processing areas in each individual. This localizer is frequently used for different studies in our lab. Since it also contains blocks of bodies, this later gave us the opportunity to also locate EBA per subject after this area caught our attention. This run comprised 20 stimulation blocks of 12s, interleaved with 14s fixation blocks. Stimulation blocks contained twelve pictures of either bodies, faces (different ones than those used in the main experiment), houses or tools, each presented for 450ms with an inter stimulus interval of 600ms. Here, a one-back task was used. Total run duration was 8m54s.

■ Data acquisition

Scanning was performed in a 3T head scanner (Siemens Allegra, AG, Erlangen, Germany) using a standard quadrature birdcage head coil. For the experimental scan, the following scan parameters were used: TR= 2250ms; TE= 25ms; 42 slices of 2.5mm (no gap); leading to a resolution of 3.5x3.5x2.5mm. For the localizer scan different parameters were used to achieve a higher resolution of 2x2x2mm: TR= 2000ms; TE= 30ms; 28 slices of 2mm (no gap).

■ Data analysis

For the fMRI data analysis BrainVoyager QX (version 1.10.4, Brain Innovation, Maastricht, the Netherlands) was used. Before statistical data analysis, data was cleared for scanner-related signal drifts and head movements, temporally high-pass filtered, transformed into Talairach (Tal) space and spatially smoothed with a 4mm Gaussian kernel. The first two scans per run were excluded from the analysis to permit T1 equilibration effects.

For the whole brain analysis, a multi-subject general linear model (GLM) was run using a regression model consisting of the nine predictors corresponding to the experimental conditions plus one for the oddball blocks. The predictor time courses used were generated on the basis of a linear model of the relation between neural activation and hemodynamic response. For our main study, a whole brain random effects ANOVA with two within-participants factors (face, scene) with three levels (neutral, fearful, scramble/triangle) was performed. Investigating this data, our attention was caught when we looked at the contrast FfFs>NfNs, showing an area that we recognized as EBA. To test whether this was indeed EBA, we performed two checks. First, we functionally localized EBA on group level with the localizer data to see whether it overlapped with the cluster. Secondly, the cluster found with contrast

FfFs>NfNs was subjected to a paired-samples t-test with the group localizer data to make sure it was indeed body selective.
Since both checks showed the body selectivity of the region, we continued with using the localizer scan to define right EBA independently per subject as region-of-interest (ROI) to be able to perform a more specialized analysis. Also, we localized FFA (faces > houses & tools), which will be discussed here to show the specificity of the effect. EBA was located with at least a FDR correction of $q<.01$; only in 2 subjects a more liberal threshold of $p<.02$ was used due to otherwise small cluster sizes. FFA ROIs were chosen with at least FDR(q)<.1 and only 1 subject at $p<.02$, to be able to get cluster sizes of 50-200 voxels. From the individually located EBAs, a subject-specific ROI-based group ANOVA (two within-participants factors (face, scene) with three levels (neutral, fearful, scramble/triangle)) was performed with the experimental data, followed by various paired-samples t-tests using SPSS (Version 15.0).

Results

Our comparison of fearful faces within a fearful scene versus neutral faces within a neutral scene at the whole brain level, revealed an area within right lateral occipito-temporal cortex. When comparing this to the body specific activation found with the separate functional localizer scan on group level, they indeed showed overlap (see Fig. 1). Similarly, comparing fearful vs. neutral scenes without faces revealed the same area. The fact that these simple effects are found at the whole brain level shows the robustness of the following ROI findings.

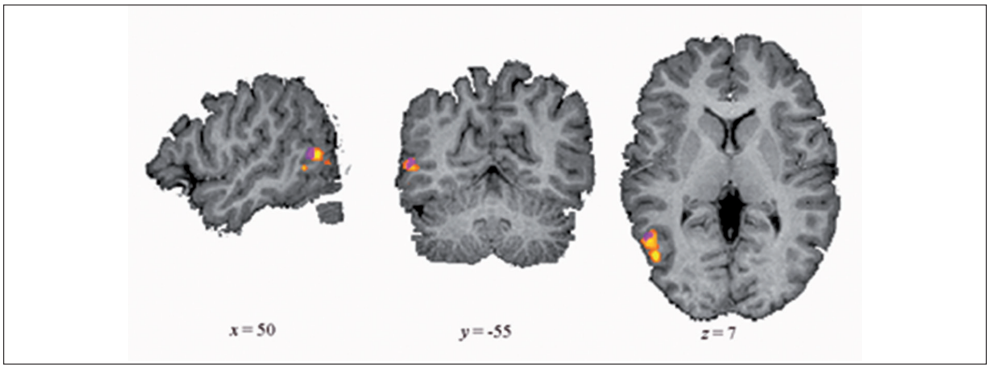

Figure 1. *Overlap between experimentally found and functionally localized EBA*. *EBA was experimentally found with contrast Fearful face in Fearful scene > Neutral face in Neutral scene on whole brain level (p<.005; purple cluster). The group activation was found for bodies > faces + tools + houses with the functional localizer (FDR (q)<.003; yellow/orange cluster).*

The additional paired-samples t-test with the localizer data in the whole brain FfFs>NfNs cluster showed that bodies gave rise to more activation in this region than faces ($t(13) = 6.130$, $p = .000$, $d = 1.079$), houses ($t(13) = 8.830$, $p = .000$, $d = 1.758$) and tools ($t(13) = 7.298$, $p = .000$, $d = 1.303$). There was no difference in activation between houses, faces and tools. This result illustrates the strong body selectivity of this cluster.

In all participants it was possible to locate EBA in the right hemisphere, and all individual Tal coordinates fell within the range of those reported in different studies as investigated in our review (de Gelder *et al.*, 2010) (see table 1 and Fig. 2).

Table 1. *All individual Tal coordinates per subject.*

Subject	x	y	z	voxels
1	40	-66	7	182
2	45	-63	1	103
3	50	-61	4	142
4	49	-66	3	128
5	44	-68	13	144
6	49	-60	5	184
7	46	-73	9	171
8	51	-64	7	121
9	48	-70	18	142
10	47	-64	5	207
11	44	-64	-2	228
13	40	-73	18	147
14	50	-63	5	200
15	49	-67	9	183

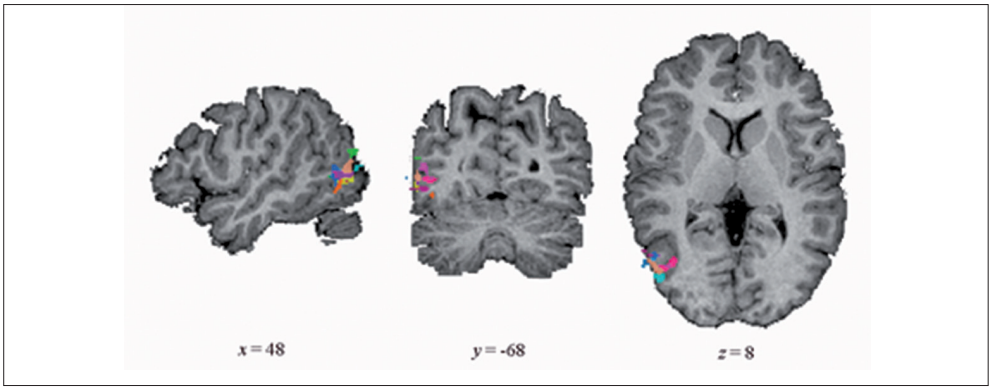

Figure 2. *All individually localized right EBA clusters.*

The subject-specific ROI-based group ANOVA showed an interaction between facial and scenery emotion ($F(4,10) = 11.309$, $p<.001$, $\eta_{p2} = .819$). Paired-samples t-tests showed that fearful faces in fearful scenes gave rise to higher activation than neutral faces in neutral scenes (FfFs > NfNs; $t(13) = 3.207$, $p = .007$, $d = .259$). This contextual emotion effect in EBA seemed to be caused by threat from the scenes (NfFs > NfNs; $t(13) = 2.958$, $p = .011$, $d = .257$), not by fear from the faces (FfNs > NfNs; $t(13) = 0.281$, p =n.s., $d = .029$). This is especially clear when looking at the stimuli without faces which produced the strongest effect; threatening scenes gave rise to higher EBA activity than neutral scenes (XfFs > XfNs; $t(13) = 5.814$, $p = .000$, $d = .658$). Also, there was a trend for more activation for fearful faces when they appeared in a fearful scene (FfFs > FfNs; $t(13) = 2.020$, $p = .064$, $d = .248$). See Figure 3 for the average hemodynamic responses within right EBA per condition.

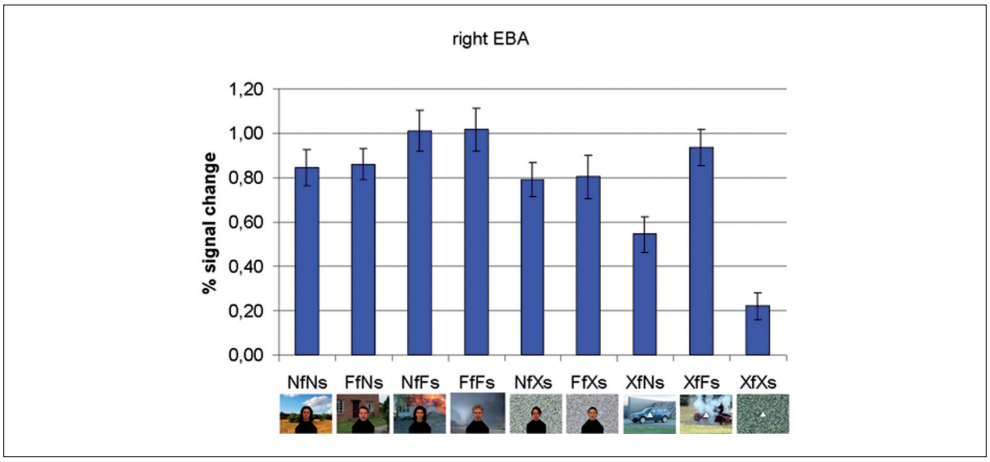

Figure 3. Subject-specific region-of-interest (ROI)-based group analysis in right extrastriate body area (EBA). *There is an interaction between facial and scene emotion. The region shows more activation for fear presented in both contexts than to no emotion at all (FfFs >NfNs: p<.007). This effect is probably caused by the emotion from the scene (NfFs > NfNs: p<.011) and not by emotion from the face (FfNs > NfNs: n.s.), especially since threatening scenes without face also activate EBA (XfFs >XfNs: p<.000). N = neutral; F = fearful; f = face; s = scene; X = control (scrambled scene or no face).*

To see whether those emotional scene effects are specific to EBA, we performed the same subject-specific ROI-based group analysis in right FFA (see Fig. 4). Here we also found an interaction ($F(4,10) = 11.258$, $p<.001$, $\eta_{p2} = .818$). However, in contrast with EBA, this was not due to higher activation specifically in case of a threatening scene. Only when there were no faces, this area responded more to fearful than neutral scenes (XfFs > XfNs; $t(13) = 3.638$, $p = .003$, $d = .491$), but this activation was still much lower than the activation for scenes including faces (whether being emotional or not). So adding a fearful face to the fearful scene increased the response in right FFA (FfFs > XfFs; $t(13) = 5.072$, $p = .000$, $d = 1.732$).

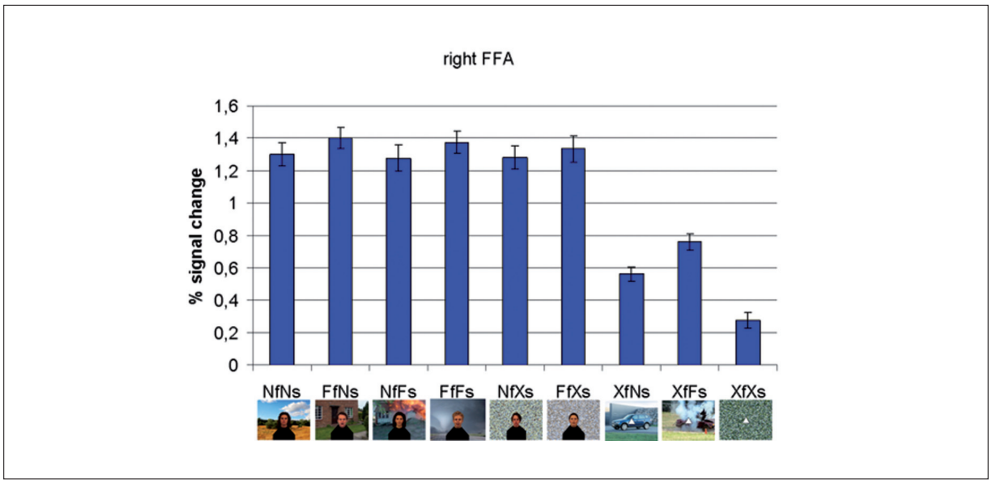

Figure 4. Subject-specific region-of-interest (ROI) group analysis in right fusiform face area (FFA). *Those were individually localized by an independent localizer run. There is an interaction between facial and scenery emotion. Adding a fearful face to a fearful scene increases activation (FfFs > XfFs: p<.000). Fearful vs. neutral scenes without faces shows higher activation in right FFA (XfFs > XfNs: p<.003). N = neutral; F = fearful; f = face; s = scene; X = control (scrambled scene or triangle).*

Discussion

Our results show that EBA can get activated solely by a threatening scene in which there is no body present. This indicates that the constructive processes of the brain go beyond merely activating the representation of a stimulus not explicitly represented. The EBA activation was specifically associated with threatening scenes since it was also observed for threatening scenes in case there was no face present, and was as high as when faces were included. Although imagination can activate the corresponding object category in the brain (Ishai *et al.*, 1999), we believe the activation found here is not simply due to imagination of the body since FFA reacted significantly less to the no-face stimuli. Also in the study of Cox and colleagues (Cox *et al.*, 2004), FFA responded to blurred faces when presented on top of a body, but not when presented in isolation. Furthermore, there was a significant difference in EBA between scene stimuli with and without faces. So, the fact that we do find EBA specifically for threatening scenes without faces may suggest that the observed EBA activation reflects associative and anticipatory capabilities of the brain. This interpretation is quite speculative, but in line with this, previous studies have shown that the brain is able to do this very quickly. Orbitofrontal cortex seems to make predictions of possible representations even before the stimulus is recognized in the corresponding

visual object processing areas (Bar *et al.*, 2006). These predictions are based on memory of past experiences, mental simulation, imagery, and contextual cues. Some even argue that the brain is actually continuously generating predictions (Bar, 2009). Also, anticipation of a stimulus has been shown to activate the same regions that are found active for the actual sensory input (Carlsson *et al.*, 2000).

Another possible explanation for the observed EBA activation needs to be explored in future work. The observed EBA activity could be related to the participant's own bodily awareness triggered by the fear scene and reflect the observer's body posture in such a case. This might explain why no EBA modulation was found in a recent study whereby subjects viewed hands either in pain or not (Lamm & Decety, 2008). As long as you yourself are not in danger, there is no need to flee. Interestingly, regions that are involved in body schema and action awareness representations are in close proximity to EBA, like the angular gyrus (Blanke *et al.*, 2002; Farrer *et al.*, 2008). And EBA itself, in addition to visual processing, also appears to integrate sensory-motor signals related to the representation of your own body, also when no real motion is involved as is the case during motor imagery (Astafiev *et al.*, 2004). In a very recent study, Kühn and colleagues found EBA activated together with hand-related areas of the motor cortex when anticipating having to make a hand movement (Kühn *et al.*, 2010). This again suggests that EBA plays a role in representing the own body. Finally, it seems to be involved in a network, together with right temporoparietal junction and posterior superior temporal gyrus, activated during out-of-body experiences (De Ridder *et al.*, 2007).

There was no condition specific effect in EBA for emotional faces. A possible reason for this may be that attention was on the whole stimulus and as the scene covers more space than the face it may have absorbed the most attention. However, we suggest that it is more plausible that a threatening scene provides more cues about bodily behavior and action than provided by an isolated fearful face. Future studies could include heart and breathing rate measurements to measure bodily responses to the threatening scene.

In conclusion, our findings possibly provide neural evidence of the role of emotional contextual cues and might indicate that the brain reacts to the meaning of the scene by projecting the bodily behavior associated with the scene. While this result was obtained by pursuing a lead provided in a fuller design, we believe it is worth reporting for its own sake. Indeed, the present result illustrates for the first time for the field of affective perception the constructive properties of the visual system which have been highlighted already for scene and object perception.

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Chapter 5

Tease or threat? Judging social interactions from bodily expressions

"Respond in accordance to your opponent."
~ Gichin Funakoshi ~

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Abstract

We casually observe many interactions that do not really concern us. Yet sometimes we need to be able to rapidly appraise whether an interaction between two people represents a real threat for one of them rather than an innocent tease. Using functional magnetic resonance imaging we investigated whether small differences in the body language of two interacting people are picked up by the brain even if observers are performing an unrelated task. Fourteen participants were scanned while watching 3s movies (192 trials and 96 scrambles) showing a male person either threatening or teasing a female one. Furthermore, in one task condition, observers categorized the interaction as threatening or teasing and in the other they monitored randomly appearing dots and categorized the color. Our results clearly show that right amygdala responds more to threatening than to teasing situations irrespective of the observers' task. When observers´ attention is not explicitly directed to the situation, this heightened amygdala activation goes together with increased activity in body sensitive regions in fusiform gyrus, extrastriate body area - human motion complex and superior temporal sulcus and is associated with a better behavioral performance of the participants during threatening situations. In addition, regions involved in action observation (inferior frontal gyrus, temporo-parietal junction and inferior parietal lobe) and preparation (premotor, putamen) show increased activation for threat videos. Also regions involved in processing moral violations (temporo-parietal junction, hypothalamus) reacted selectively to the threatening interactions. Taken together, our results show which brain regions react selectively to witnessing a threatening interaction even if the situation is not attended because the observers perform an unrelated task.

Introduction

When walking along busy streets, we are often surrounded by people engaged in intense interactions. The casual observer witnesses these without paying much attention. Yet sometimes a scene between two people that looks like a playful tease may in fact be an aggression. Rapid discrimination of whether we witness another person being teased or aggressed will prompt an observer either not to get involved or to be of assistance to the potential victim. Our goal was to find out whether observers pick up small differences in the body language of two interacting people allowing them to tell whether their interaction is just about teasing or represents a real menace, and how this is reflected in condition specific brain activations.

Research on bodily expressions is a relatively new field in cognitive neuroscience. Available literature shows that fusiform gyrus (FG) and amygdala (AMG) play

an important role in perceiving bodily expressions, as well as other areas that are closely related to emotional processes like orbitofrontal cortex (OFC) and insula (Hadjikhani & de Gelder, 2003, de Gelder *et al.*, 2004) (for an overview, see (de Gelder, 2006)). This emotion-related activation co-occurs with activation of areas involved in representation of action and movement including the inferior frontal gyrus (IFG), supplementary motor area (SMA), caudate nucleus and putamen. Additionally, activation found in areas related to stimulus detection/ orientation (superior colliculus (SC) and pulvinar) appears compatible with models postulating a rapid, automatic route for fear detection (LeDoux, 1992).

Some recent studies of bodily expressions have used dynamic stimuli and have proven useful for better understanding the respective contribution of action-related and emotion components. For example, a study by Grosbras and Paus (2006) showed that video clips of angry hands triggers activations that largely overlap with those reported for facial expressions in the FG. Two event-related functional magnetic resonance imaging (fMRI) studies have been performed with fearful and angry whole body expressions in movies (Grèzes *et al.*, 2007, Pichon *et al.*, 2007). The movies showed someone opening a door in either a fearful/angry way or a neutral way and the role of the dynamics was clarified when activations were compared with those for static pictures. Both studies found an interaction between the emotion and movement in the superior temporal sulci (STS) and right premotor cortex (PM) with more activation for fear/anger than for neutral, but only when dynamic information was present. These results indicate that these areas probably represent the perceived emotional action.

All studies mentioned so far use bodily expressions shown by a single actor, but our everyday life evolves around observing and participating in interactions including multiple agents. To address this novel issue we selected a familiar situation involving two people and showing a male actor either teasing or threatening a female. Our first prediction was that observing a threatening compared to a teasing situation will trigger more AMG responses in the observer. Secondly, related to this, previous investigations of the role of attention have suggested that emotional signals are processed even when attention is engaged elsewhere because threat signals are perceived automatically and independently of attention (Dolan & Vuilleumier, 2003, Tamietto *et al.*, 2007). An alternative view is that attention is a prerequisite for processing emotional information as it requires that attentional resources be available (Pessoa *et al.*, 2005). Here we predicted that even when involved in an attention demanding task, which may reduce the available cortical resources, observing a threat interaction still triggers AMG more than a teasing situation.

A third prediction involves the role of body processing areas in FG, lateral occipitotemporal cortex (extrastriate body area (EBA) -human motion complex (hMT+/V5)) and STS. It is presently not known whether these areas are involved in processing interactions, and if so, whether they react differentially to the type of

interaction observed. Since FG and AMG have consistently been found in many face and body studies (Adolphs, 2003, Hadjikhani & de Gelder, 2003), we also expected this area to be more activated for threat than tease in general. Plus, we expected that when AMG reacts to the threat in the attention demanding task, this information will be passed through to FG, leading also to more activation for threat than tease in this condition. Additionally, we expected EBA-hMT+/V5 and STS to be more responsive to threat than tease in general, a result which was found with angry and fearful body movements (Grèzes *et al.*, 2007, Pichon *et al.*, 2007).

Furthermore, we also explored the relation between emotion and action representation. Observing the interacting bodies will lead to an imitative response tendency – as behavioral studies have found (Brass *et al.*, 2001) – and possibly trigger regions involved in action representation and preparation. These regions – which includes PM, inferior frontal gyrus (IFG; Brodmann's areas (BA) 44/45), rostral inferior parietal lobe (IPL), and STS – are likely to be more responsive when the actions are threatening as found by previous studies (de Gelder *et al.*, 2004, Pichon *et al.*, 2007, Grèzes *et al.*, 2007), and it might even be the case when the threat is not directly aimed towards the observer because a defensive reaction might still be necessary in case the attacker decide to also turn against you. Also, it seems adaptive to have this mechanism operational automatically even if we engage in an attention demanding task (Brass *et al.*, 2001).

Finally, in contrast with almost all previous studies exposing participants to affective stimuli, the role of our participants is clearly defined as being a witness of an interaction of which they are not part. Like in everyday life, the observer may more or less empathize with the victim or be more or less indifferent to what goes on around him. In line with this, we expected areas involved in moral cognition – including anterior temporal pole (TP), medial prefrontal cortex (PFC) and OFC (Moll *et al.*, 2008, Zahn *et al.*, 2009) – to be activated during the movies where attention is explicitly on the situation. Furthermore, when this situation is threatening, it may activate PFC and OFC even more, as well as insula, hypothalamus and temporo-parietal junction (TPJ) as found in studies for moral violations (Berthoz *et al.*, 2002, Moll *et al.*, 2008, Zahn *et al.*, 2009).

Methods

■ Participants

Fourteen healthy volunteers (five male; 23.6 ± 5.1 years; all right-handed) participated in this experiment after providing a written informed consent. All participants had normal or corrected-to-normal vision. The study was performed in accordance to the *Declaration of Helsinki* and was approved by the local medical ethical committee.

■ Materials

Fourteen students (seven male) of the Tilburg University were filmed while they were engaged into a social interaction which always involved one male and one female. The male actor was trying to grab the handbag of the female actor and did so either in a playful way or aggressively. In the latter case, the male expressed anger and the female expressed fear.

The raw footage was edited into 3s movies (484 x 504 pixels; 25 frames/second; 209kbps data rate; 24 bit sample size; compressed by Indeo video 5; 11.5 x 12 cm on screen) using Ulead VideoStudio (version 10) and processed with Adobe After Effects (version 6). Editing comprised blurring of the faces, converting the videos into black/white and, in a later stage, putting a colored dot in three frames (40ms, visual angle = 0.3˚) of each movie. Furthermore, a scrambled version of each movie was made by performing a Fourier transformation in Matlab (version 7.4) whereby phases of each RVB layer were scrambled. The scrambling has been kept constant for each movie so that we did not induce any differential scrambling between layers and frames.

The edited movies were validated by a group of different participants using a forced-choice response (threatening *vs.* teasing) and they were also rated on emotional intensity. For the final experiment, twelve actor combinations which had the best recognition rates (M = 87.7%, SD = 13.29) were selected. Each actor combination appeared in every stimulus condition. However, two different stimuli sets were created so that one and the same male actor was always either an aggressor or a teaser for one subject, in order to make the situation more realistic.

■ Design and procedure

A slow event-related design was used with enough time between the separate movies for the BOLD response to largely return to baseline. After each 3s movie, an answer screen appeared for 2s, followed by a fixation interval of 11s (see Figure 1).

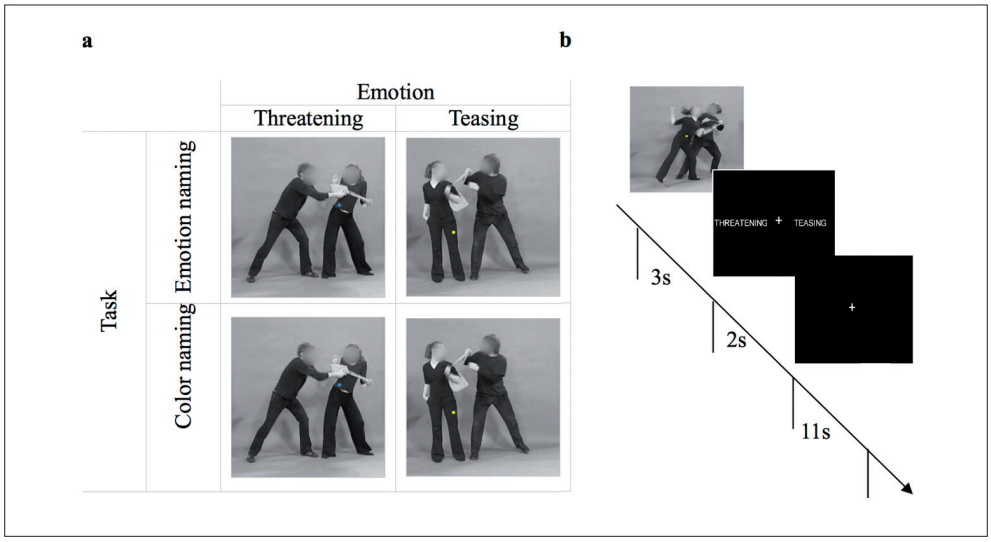

Figure 1. *Design of the fRMI study and example of a trial. (a) 2 * 2 factorial design. 3s movies of a man grabbing the handbag of a woman were identical in the emotion naming and the color naming task. (b) Example of a trial. After each movie, an answer screen appeared for 2s instructing the participants to make a forced choice, followed by a fixation cross for 11s until the start of the next movie.*

Every session comprised four functional runs. There was one task per run in order to prevent confusion to the participants. During the color naming task participants had to ignore what happened in the movies and pay attention to three colored dots that appeared during those movies. The dots could be blue or yellow and the participants had to make a forced-choice of whether those dots were of the same or of different colors. The dots always appeared somewhere on the bodies in order to minimize the shifts in spatial attention across conditions. During the emotion naming task participants had to pay attention to the actors in the movies and they had to make a forced-choice of whether the situation was threatening or teasing. On the following answer screen the response alternatives appeared randomly left or right of the fixation cross so that participants had to withhold their response until after the movie in order to avoid motor anticipation related effects.

Stimuli were presented using Presentation software (Neurobehavioral Systems, Inc, version 11.0). The participants had to perform both tasks twice in two runs each, with an anatomical scan in the middle.

A total of 288 trials (including 96 scrambled videos) were presented. All stimuli (12 threatening, 12 teasing videos) were presented twice per run and the scrambled movies only once. Each functional run contained 72 trials. Every stimulus was synchronized to a trigger from the scanner, so each movie started at the same time as a new scan volume.

All stimuli were generated by a PC and projected onto a frosted screen located at the end of the scanner bore (at the side of the participants' head) with a liquid crystal display (LCD) projector (PLC-XT11-16, Sanyo North America Corporation, San Diego, USA). The participants viewed the stimuli via a mirror mounted to the head coil at an angle of ± 45°.

■ fMRI data acquisition

The MRI unit used was a commercial head scanner with a magnetic field strength of 3T (Siemens Allegra, AG, Erlangen, Germany) provided with a standard quadrature birdcage head coil. Foam padding placed around the head was used to minimize movement and the participants were provided with ear plugs to reduce the scanner noise.

In each session, after a first quick nine-slice localizer for orientation, a three-dimensional (3D) T1-weighted data set was scanned using parameters from the Alzheimer's Disease Neuroimaging Initiative (ADNI) encompassing the whole brain (scan parameters: repetition time (TR) = 2250ms, echo time (TE) = 2.4ms, flip angle (FA) = 9°, field of view (FOV) = 256 × 256mm^2, matrix size = 256 × 256, number of slices = 192, slice thickness = 1mm, no gap, total scan time = 8m and 5s).

The scan parameters of the functional sequence used were: TR = 2000ms, TE = 30ms, FA = 90°, matrix size = 64 × 64, FOV = 224 × 224mm^2, slice order = descending-interleaved, slice thickness = 3.5mm (no gap), number of volumes = 583 for the color naming runs (total scan time = 19m and 26s), 559 for the emotion naming runs (total scan time = 18m and 38s). The emotion naming runs were a bit shorter than the color naming runs because the scrambled movies were not followed by an answer screen in the former.

■ Behavioral data analysis

To test whether performance on the emotion *vs.* color naming task was different for the threatening *vs.* teasing movies, a planned comparison was performed with a paired-samples t-test in SPSS (version 15.0 for Windows). Also, a repeated measures univariate analysis of variance (ANOVA) was performed with two factors (emotion - task) and two levels (threatening/teasing - emotion naming/color naming) to see whether there was a difference in performance between the two tasks.

■ FMRI data analysis

For the fMRI data analysis BrainVoyager QX (version 1.9 Brain Innovation, Maastricht, the Netherlands) was used. A number of preprocessing steps were performed on the functional data. These included incremental linear trend removal to eliminate scanner-related signal drifts; temporal high-pass filtering to remove temporal frequencies lower than 3 cycles per run; and a rigid body algorithm which

rotates and translates each functional volume in 3D space in order to correct for small head movements in between scans. For the group ANOVA on the volume and the surface, the data was spatially smoothed with a 4mm Gaussian kernel. To enable the comparison between participants, all anatomical as well as functional volumes were spatially normalized into Talairach space. The first two scans per run were excluded from the analysis to permit T1 equilibration effects. The 3D T1-weighted scans were used to overlay the statistical maps on for anatomical orientation.

At single-subject level, fixed-effects whole brain ANOVAs were performed using a regression model consisting of the eight predictors corresponding to the particular experimental conditions (threatening and teasing expressions of the actors in the two task conditions and the scrambled versions of the four stimulus conditions) plus a ninth for the response period. The predictor time courses used were generated on the basis of a linear model of the relation between neural activation and hemodynamic response. Furthermore, regions of interest (ROIs) were localized by contrasting all movies versus their scrambled counterparts using a conjunction analysis approach. This way, we aimed to define the following regions per subject: FG, EBA-hMT+/V5 and STS. They were chosen with relatively liberal uncorrected criterion (minimum $p < .05$, 200-600 voxels). The AMG was anatomically defined. Beta-values from the ROIs were extracted from BrainVoyager into SPSS (Version 15.0) in order to perform a random effects ANOVA to look for main effects of emotion and task and for interaction effects. In case of an interaction, paired-samples t-tests were performed to look specifically at both tasks and both emotions separately.

At group level, a single subject ROI-based group ANOVA with two within-participants factors (emotion x task) with two levels (threatening/teasing – emotion naming/color naming) had been performed. Secondly, a whole brain random effects ANOVA with the same factors was performed to exploratory look for the main effects of emotion and task and for interaction effects. The resulting volume maps per contrast were subjected to a cluster-level statistical threshold analysis in order to correct for multiple comparisons (Forman *et al.*, 1995, Goebel *et al.*, 2006). Additionally, after segmenting the grey from the white matter from each individual brain, a cortex-based alignment was performed with all brains separately for the left and right hemisphere to reduce individual macro-anatomical differences between subjects. While the algorithm uses curvature information as its cost function, it effectively aligns homologue gyri and sulci across subjects. One person was excluded from this analysis since the anatomical scan was too blurry for segmentation due to extensive head motion. An average segmented (surface-based) brain representation was created after alignment on which a random effects ANOVA had been performed with the same predictors as before. Also with the resulting volume maps, cluster-level statistical threshold analyses had been performed.

For the analysis within the ROIs, a threshold of $p < .05$ was used. The whole brain analyses were corrected for cluster-size. Only the group results are reported.

Results

■ Behavioral results

Threatening situations were well recognized as shown in the average recognition rates during the emotion naming task (M = 83.9%, SD = 11.15) and participants also performed well in the color naming task (M = 90.8%, SD = 8.32) (see Figure 2). A repeated measures ANOVA showed that there was an emotion effect ($F(1,10)$ = 5.455, p =.042, η_{p2} = .353) as well as a task effect ($F(1,10)$ = 13.875, p = .004, η_{p2} = .581) indicating that recognition rates were highest in the color naming condition and for threatening movies.

Although there was no interaction, the planned comparison showed that participants performed the color naming task better when there was a threatening situation in contrast to a teasing one ($t(12)$ = 3.051, p =.010, d = 1.056).

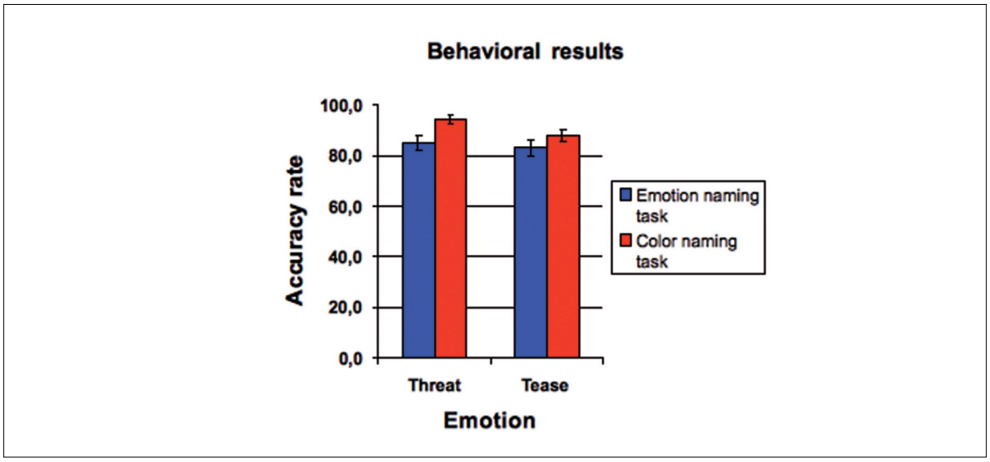

Figure 2. *Behavioral results. Mean accuracy rates for threatening and teasing movies during both tasks. Participants performed the color naming task better than the emotion naming task, and they performed the color naming task better during threatening than teasing movies.*

■ FMRI results

ROI analysis

It was possible to locate in almost every subject the ROIs we were interested in. However, it was only possible to locate left STS in less than half of the participants, which is not surprising since more studies found this right hemisphere STS lateralization for biological motion perception (Bonda *et al.*, 1996, Beauchamp *et al.*, 2003). Table 1 shows the average Talairach coordinates per ROI and table 2 shows the individual Talairach coordinates for the main regions.

An emotion effect was found in right AMG, with more activation for threatening than teasing interactions ($F(1,13) = 6.024$, $p = .029$, $\eta_{p2} = .32$). In left AMG no effects were found.

Left FG ($F(1,13) = 6.453$, $p = .025$, $\eta_{p2} = .33$) showed an interaction effect between emotion and task (see Figure 4). Right FG showed a trend towards interaction ($F(1,13) = 3.942$, $p = .069$, $\eta_{p2} = .23$) and a main effect for task with more activation during the emotion than color naming task ($F(1,13) = 25.651$, $p<.001$, $\eta_{p2} = .66$). T-tests revealed bilaterally a difference between threatening and teasing in the color naming task (left: $t(13) = 3.819$, $p = .002$, $d = .25$; right: $t(13) = 3.181$, $p = .007$, $d = .42$).

Bilateral EBA-hMT+/V5 showed a main effect of emotion (more activation for threatening than teasing interactions) (left: $F(1,13) = 9.561$, $p = .009$, $\eta_{p2} = .42$; right: $F(1,13) = 8.486$, $p = .012$, $\eta_{p2} = .40$) and a main effect for task (more activation during emotion than color naming task) (left: $F(1,13) = 9.418$, $p = .009$, $\eta_{p2} = .42$; right: $F(1,13) = 11.201$, $p = .005$, $\eta_{p2} = .46$). Furthermore, right EBA showed a trend towards interaction ($F(1,13) = 4.532$, $p = .053$, $\eta_{p2} = .26$). Therefore, we performed a t-test which revealed a difference between threat and tease in the color naming task ($t(13) = 3.355$, $p = .005$, $d = .35$).

Bilateral STS showed a main effect of task: both show more activation during the emotion than color naming task (left: $F(1,5) = 10.718$; $p = .022$, $\eta_{p2} = .68$; right: $F(1,13) = 40.576$, $p < .001$, $\eta_{p2} = .79$). Additionally, right STS showed an interaction ($F(1,13) = 5.291$, $p = .042$, $\eta_{p2} = .33$). A t-test showed a difference between threatening and teasing in the color naming task ($t(13) = 4.290$, $p = .001$, $d = .37$).

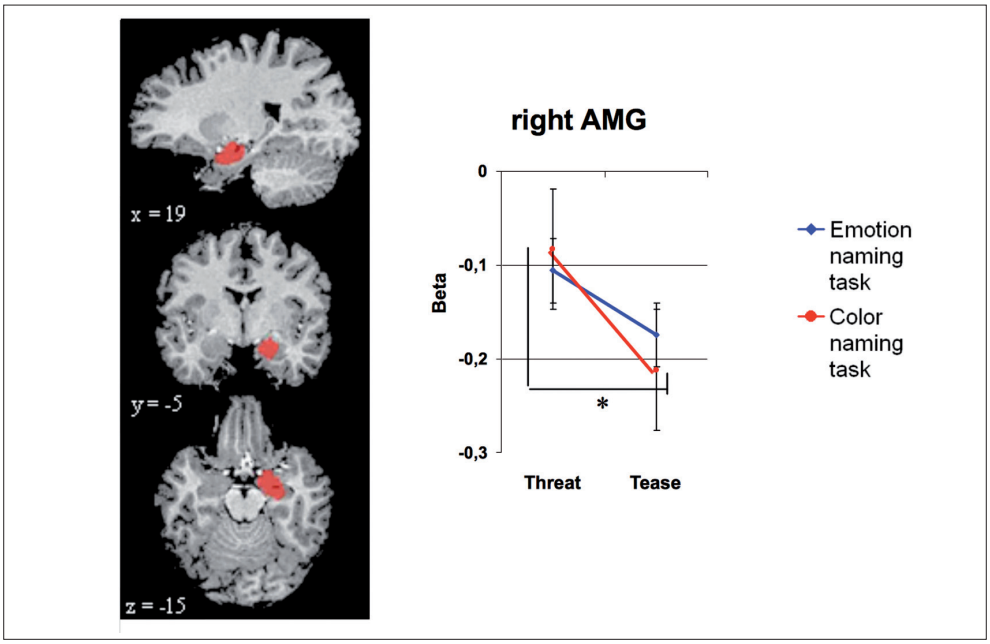

Figure 3. *Single subject ROI-based group random effects analysis in the right AMG (separate ROIs per subject clustered together here, see Table 2 for exact Talairach coordinates; neurological convention). AMG is more responsive to threatening than teasing situations during the color naming task.*

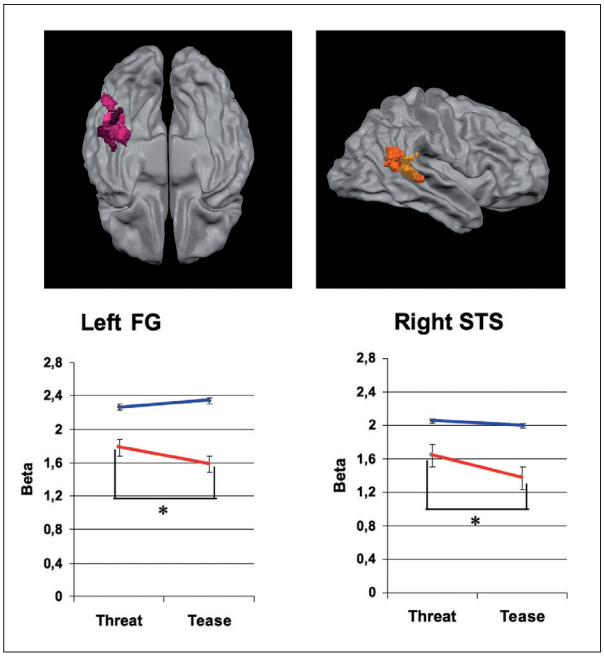

Figure 4. *Single subject ROI-based - group random effects analysis in left FG and right STS. The averaged brain representation shows the individual ROIs per subject (exact Talairach coordinates can be found in Table 2). The plots show the activation during both emotions during both tasks. Threatening movies gave rise to more activation than teasing movies during the color naming task ($p < .002$ for left FG and $p < .001$ for right STS).*

Table 1. *Average Talairach coordinates for all ROIs as found with the localizer.*

Region	*Hemisphere*	x *(SD)*	y	z
EBA	L	-46 *(3.8)*	-68 *(5.3)*	4 *(3.8)*
EBA	R	45 *(3.0)*	-65 *(3.6)*	1 *(4.7)*
FG	L	-39 *(4.6)*	-44 *(6.8)*	-15 *(3.5)*
FG	R	37 *(2.9)*	-43 *(7.0)*	-13 *(4.5)*
STS	L	-50 *(5.4)*	-41 *(7.8)*	17 *(7.2)*
STS	R	50 *(4.0)*	-38 *(7.7)*	14 *(4.3)*
AMG	L	-18 *(4.0)*	-6 *(4.3)*	-16 *(1.4)*
AMG	R	18 *(2.4)*	-5 *(3.6)*	-16 *(1.7)*

Left STS was located in only 6 subjects, right STS was located in 12 subjects.

Table 2. *Single subject Talairach coordinates for left fusiform gyrus (FG) and right posterior superior temporal sulcus (STS) as found with the contrast movies vs. scrambles. Right amygdala (AMG) was found anatomically.*

left FG					right STS				
Subject	x	y	z	voxels	*Subject*	x	y	z	voxels
1	-32	-48	-13	222	1	52	-37	10	1010
2	-33	-41	-21	390	2	51	-34	17	151
3	-42	-62	-13	507	3	50	-49	16	758
4	-41	-39	-14	440	4	Not localizable			
5	-39	-39	-17	275	5	Not localizable			
6	-31	-37	-19	279	6	52	-47	22	992
7	-42	-44	-13	209	7	51	-30	8	627
8	-36	-47	-9	391	8	58	-22	15	251
9	-43	-38	-14	325	9	50	-19	-5	674
10	-47	-41	-14	218	10	50	-40	10	126
11	-37	-50	-18	357	11	44	-34	9	138
12	-37	-42	-17	390	12	53	-37	19	396
13	-40	-42	-9	187	13	50	-37	15	194
14	-42	-51	-12	170	14	43	-44	17	471

right AMG				
Subject	x	y	z	voxels
1	15	-5	-16	285
2	19	-4	-15	514
3	16	-4	-16	333
4	18	-3	-19	263
5	17	0	-17	297
6	16	-3	-15	352
7	17	-5	-16	314
8	17	-5	-13	282
9	16	-3	-15	307
10	20	-8	-12	345
11	17	0	-17	421
12	20	-5	-17	209
13	18	-10	17	379
14	24	-12	15	395

Whole brain analysis

An overview of the results of the whole brain analysis is provided in Figure 5-6 and Table 3 to 5.

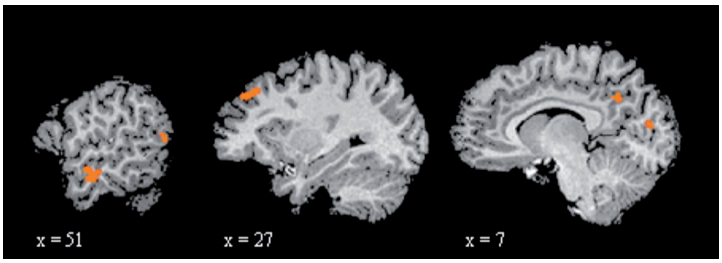

Figure 5. *Group results of interaction (between emotion and attention) effect with whole brain analysis (p < .05, cluster-size corrected). Shown are right anterior STS, MOG, SFG, PCC and cuneus.*

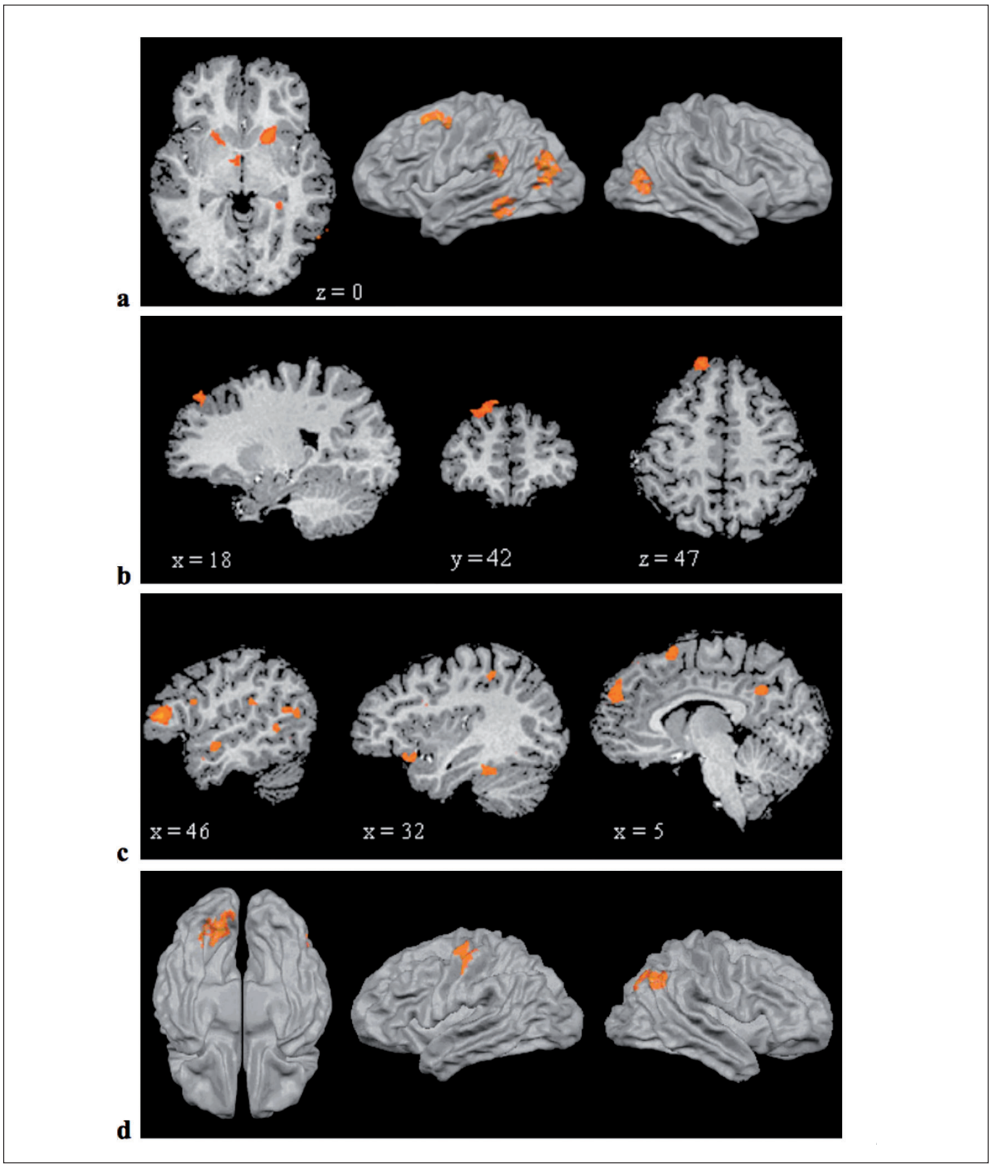

Figure 6. *Group results of main effects with whole brain analysis (neurological convention). (a) Main effect of emotion: threat vs. tease ($p < .045$, cluster-size corrected). Shown are putamen, hypothalamus/basal forebrain, hippocampus, PM, TPJ, MTG and EBA-hMT+/V5. (b) Main effect of emotion: tease vs. threat ($p < .045$, cluster-size corrected). Shown is superior frontal gyrus (BA8). (c) Main effect of task: emotion vs. color naming ($p < .012$, cluster-size corrected). Shown are anterior temporal pole, anterior STS, EBA-hMT+/V5, IFG, MTG, TPJ, OFC, FG, postcentral sulcus, medial PFC, and PCC. (d) Main effect of task: color vs. emotion naming ($p < .032$, cluster-size corrected). Shown are V4, pre- and postcentral gyrus and IPL.*

Table 3. *Interaction between emotion and task as found with whole brain ANOVA.*

Interaction:

Region (BA)	*Hemisphere*	x	y	z
Cuneus (19)	L	-2	-76	30
Cuneus (18)	R	5	-77	14
Posterior cingulate cortex (19)	L	-7	-51	30
Posterior cingulate cortex (31)	R	11	-51	32
Inferior frontal gyrus (45)	L	-40	48	-3
Superior frontal gyrus (8/9)	R	27	36	39
Middle occipital gyrus (19)	R	49	-65	17
Anterior superior temporal sulcus (38)	R	49	-12	-11

$p < .05$, cluster-size corrected.

Table 4. *Main effect of emotion as found with whole brain ANOVA.*

Threat > tease:

Region (BA)	*Hemisphere*	x	y	z
Putamen	L	-18	10	-2
Putamen	R	18	7	-4
Inferior occipital gyrus (19)	L	-45	-63	-12
Inferior parietal lobe (19)	L	-40	-69	36
Posterior cingulate cortex (31)	L	-10	-39	36
Fusiform gyrus (20)	L	-40	-38	-14
Hippocampus	L	-36	-37	-2
Hypothalamus/basal forebrain	R	4	-6	-7
Temporoparietal junction (42)	R	50	-31	20

Tease > threat:

Region (BA)	*Hemisphere*	x	y	z
Superior frontal gyrus (8)	R	18	42	47

$p < .045$, cluster-size corrected.

Table 5. *Main effect of task as found with whole brain ANOVA.*

Emotion > color naming:

Region (BA)	*Hemisphere*	x	y	z
Medial prefrontal cortex (6)	L	-4	19	57
Medial prefrontal cortex (6)	R	13	35	50
Medial prefrontal cortex (6)	R	5	12	58
Medial prefrontal cortex (8)	L	-4	29	44
Medial prefrontal cortex (10)	R	8	52	31
Inferior frontal gyrus (45)	L	-44	34	9
Inferior frontal gyrus (44)	R	48	31	15
Inferior frontal sulcus (44)	R	41	9	26
Orbitofrontal gyrus (47)	L	-42	22	0
Orbitofrontal gyrus (11)	R	33	21	-11
Medial temporal gyrus (19)	L	-45	-56	11
Inferior Temporal Sulcus (19)	R	51	-48	7
Temporoparietal junction (40)	L	-60	-34	28
Temporoparietal junction (42)	R	50	-31	25
Fusiform gyrus (20)	L	-39	-33	-15
Fusiform gyrus (20)	R	35	-34	-17
Temporal pole (38)	R	45	10	-19
Postcentral sulcus (7)	R	30	-36	45
Posterior cingulate cortex (31)	R	5	-51	33
Posterior superior temporal gyrus (38)	R	44	-2	-8
Inferior occipital gyrus (18)	R	40	-61	-5
Middle occipital gyrus (19)	R	45	-59	17

Color > emotion naming:

Region (BA)	*Hemisphere*	x	y	z
Dorsal postcentral gyrus (7)	L	-49	-14	49
Dorsal postcentral sulcus (7)	R	49	-14	51
Putamen	L	-24	2	5
Putamen	R	23	2	5
Calcarine sulcus (18)	L	-3	-76	13
Cuneus (18)	R	5	-72	13
Medial occipitotemporal gyrus (17)	L	-8	-72	-9
Medial occipitotemporal gyrus (19)	R	3	-75	-7
Superior frontal gyrus (6)	Bilateral	1	-5	56
Dorsal precentral gyrus (4)	L	-2	-29	54
Ventral precentral gyrus (6)	R	57	-4	24
Supramarginal gyrus (39)	R	48	-43	45

Emotion *vs.* color naming ($p < .012$) and color *vs.* emotion naming ($p < .032$), both cluster-size corrected.

Regions showing an interaction between emotion and task. The whole-brain analysis showed an interaction between emotion and task in the cuneus, posterior cingulate cortex (PCC), left IFG (BA45/pars triangularis), left superior frontal gyrus (SFG), right anterior STS and right middle occipital gyrus.

Activation related to observing either a threatening or a teasing situation independent of the task. The whole-brain analysis with contrast threatening *vs.* teasing movies revealed bilateral putamen and inferior occipital gyrus (IOG), IPL, hippocampus and PCC in the left hemisphere. In the right hemisphere hypothalamus/ basal forebrain and TPJ were found. In addition, the surface-based analysis revealed PM, inferior temporal sulcus (ITS) and middle temporal gyrus (MTG) in the left hemisphere. In contrast, observing a teasing situation independent of the task only showed activation in right superior frontal gyrus (SFG).

Activation related to emotion naming independent of the emotion condition. Regions activated during the emotion naming task, independent whether it was a threatening or a teasing situation, were dorsomedial and dorsolateral PFC, OFC, IOG, TPJ and ITS. In addition, only in the right hemisphere we found superior anterior TP, occipitotemporal sulcus, postcentral sulcus and PCC. Additionally, the surface-based analysis also showed bilateral SFG and anterior STS in the right hemisphere.

Activation related to color naming independent of the emotion condition. Regions activated during the color naming task were dorsal postcentral gyrus, putamen, cuneus and medial SFG. In the left hemisphere also superior temporal gyrus (STG) and dorsal precentral sulcus got activated and in the right hemisphere ventral precentral gyrus and supramarginal gyrus.

Discussion

Our goal was to investigate the brain regions associated with witnessing an interaction between two people in which one person threatens the other and whether explicitly paying attention to the situation makes a significant difference. Our major results are that right AMG is active in the attended as well as unattended threat condition while the body processing regions FG, EBA-hMT+/V5 and STS only for unattended threat. In contrast, left IFG responds specifically to threatening stimuli when attention is explicitly on the content of the movies. Right TPJ and hypothalamus, as known to be involved in processing moral violations, were found activated here for threatening situations. We discuss each aspect in turn.

The automatic role of AMG for witnessing threatening interactions

Our first hypotheses were about whether witnessing a threatening interaction between two people as an external observer will trigger AMG activity and whether this activation will remain when the observer is not paying attention to the nature of the situation but to an irrelevant detail. As predicted our results clearly indicate that witnessing a threatening situation involving two other people is sufficient to trigger AMG. And, more importantly, this is the case for both witnessing it explicitly and also when witnessing it while attention is turned away from what happens in the social interaction. This result is consistent with the notion that a threat stimulus may still be processed when no attention is paid to it. Previous studies have reported contradictory results concerning the automaticity of the AMG response to threatening stimuli. Some studies found AMG in attended as well as unattended trials (Vuilleumier *et al.*, 2001), while other researchers argue that AMG is only observed when the task in the unattended condition is not difficult or not attention engaging enough and leaves resources available for processing the threatening stimuli (Pessoa *et al.*, 2002), and still others believe the AMG actually prefers unattended threatening stimuli (Williams *et al.*, 2005). It is worth noting that previous studies used still facial images, and of course we cannot directly compare our task with those of other studies but our results are more in line with the view that the right AMG gets automatically activated for threatening stimuli, also when performing an attention-grabbing task. This also seems in line with the finding that fearful bodies presented in the neglected left visual field of patients with right-sided parietal lesions were detected more often than when those bodies were happy (Tamietto *et al.*, 2007). The finding that our effect was not bilateral is consistent with the literature (Williams *et al.*, 2005), and additionally, right AMG has been shown to be involved in avoidance behavior in contrast to approach behavior in the left AMG (Davidson & Sutton, 1995).

During unattented threat there is more processing in body processing regions than during unattented tease

Besides right AMG, the body processing regions FG, EBA-hMT+/V5 and STS also seem to be important for the processing of threat during inattention; they all show more activation for threatening than teasing situations during the color naming task. This was most explicit in left FG and right STS were an interaction was found, but there was also a trend in right FG and right EBA-hMT+/V5. Possibly, AMG detects the threat and passes this information on to these regions. Monkey data showed that the AMG also receives visual input from visual regions and the STS (Stefanacci & Amaral, 2000). Perhaps, this higher responsiveness in the body processing regions and right AMG during threatening than teasing situations leads to heightened attention to the stimuli and better processing of the movies and therefore also to a better detection of the colored dots. This may explain the better behavioral performance of the participants

during the threatening movies in the color naming task. This is also consistent with early attention cueing paradigms. When attention is already at the location where the dot is presented, subjects will be faster to detect it (Posner *et al.*, 1978).
Nevertheless, there was more activation in those regions for both types of situations during the emotion than color naming task, which is in line with other studies (Grèzes *et al.*, 2007, Pichon *et al.*, 2007) and consistent with the finding that activation in regions involved in the perception of several classes of visual stimuli, in this case bodies, are reduced or even eliminated when participants are engaged in a separate task that requires focused attention (Vuilleumier *et al.*, 2001, Chong *et al.*, 2008). Why we do not find a difference between threatening and teasing movies during the emotion naming task, could be explained by other studies that find attenuation of emotional responses during conscious evaluation, possibly mediated by right PFC (Hariri *et al.*, 2000), which we actually do find to be activated more during the emotion than color naming task. Another possibility may be that a movie gives a participant more information than a still picture and because of the task demands, participants are actively trying to search for a threat in each movie or try to imagine each movie as a threat what already puts the activation level at a higher level, while at the color naming task the participants are more naive.

■ Seeing a threatening interaction triggers more action perception

Besides STS, we were also interested in how the other regions of the action observation network reacted to our experimental conditions. Left IFG – more specifically, BA45/ pars triangularis – showed an interaction between emotion and task; it was more responsive for threatening than teasing situations during trials whereby attention was explicitly on the bodies, while this emotion effect disappeared during the other task (see Figure 7). This indicates that the emotional content in the dynamic bodies is not processed automatically in this region. Left IPL and left PM showed in general more activation for threatening than teasing situations. However, PM was more responsive during the color naming task. Apparently, when observers do not attend to the emotion, PM gets activated automatically. On the other hand, it could also be that the effect is caused by less activation during the emotion naming task as an inhibition of the natural tendency to respond as a consequence of depression of emotion related areas during explicit judgment of emotion (Hariri *et al.*, 2000).
TPJ also plays a role in biological movement and action perception (Allison *et al.*, 2000). In this study this area seems to have an emotional as well as an attentional role; in both hemispheres it is activated more when attention is directed explicitly at the situation, while only the right side is also more responsive to threatening situations. Other studies have shown that this area is also part of a network related to attending to social stimuli that potentially are of behavioral significance (Corbetta & Shulman, 2002).
These findings lead us to suggest that threatening actions, although not directed at the observer, lead to more action perception.

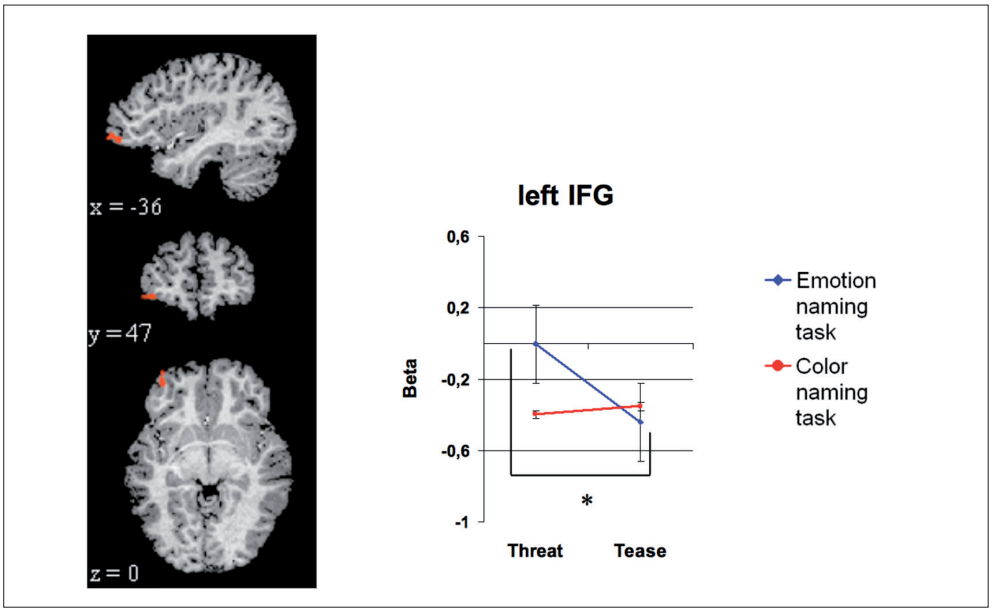

Figure 7. *Interaction between emotion and task in left anterior IFG (BA45 - pars triangularis); neurological convention. There is more activation for threatening than teasing in the emotion naming task ($p < .004$).*

■ Moral dimension of recognizing interactions

We expected that making an overt decision about the situation would activate regions involved in moral cognition. Indeed, we did find anterior TP, TPJ, different foci in medial PFC and OFC. One interpretation consistent with the literature is that in the course of labeling the interaction, the participants are trying to figure out what the situation exactly means and are trying to ascribe intentions to the people involved. One may view this categorization as related to theory of mind tasks that activate the more anterior part of STS and TP (Castelli *et al.*, 2000, Gallagher *et al.*, 2000, Saxe & Kanwisher, 2003), two regions that we also found activated in the right hemisphere for the contrast emotion *vs.* color naming task. Furthermore, both regions are also involved in retrieval of autobiographical memories (Maguire *et al.*, 2000), information which may be used to understand the actions of the people in the movies. Sensory and limbic information is send to the TP and patients with a lesion in this region show impairments in naming human actions (Lu *et al.*, 2002). However, other studies have also reported that TP is involved in processing emotional actions with both static and dynamic stimuli (Grèzes *et al.*, 2007), but we do not find this region to be activated more for threatening *vs.* teasing interactions in this study. However, teasing is not exactly the same as being emotional neutral, so it is not surprising that the results do not show a difference here.

Using verbal statements, (Moll *et al.*, 2008) found anterior PFC, hypothalamus and

anterior cingulate cortex responsive during compassion; and also anterior PFC, hypothalamus and OFC during indignation, both moral feelings that our stimuli may trigger. Among these regions, we found PFC and OFC to be activated more during the emotion naming task for both threatening and teasing situations. Only hypothalamus was differentially activated for threatening *vs.* teasing stimuli.

TPJ was already mentioned above in relation to action perception. Besides that, TPJ activity has also been reported in combination with left FG in a study that compared brain activations for hearing verbal stories about intentional violations of social norms with stories about normal behaviour (Berthoz *et al.*, 2002). Both regions are also found activated in our study for threatening situations, so the TPJ activation may also be triggered by the knowledge that stealing a handbag is an intentional violation, instead of being mere action perception.

■ Activation related to observing a threatening situation independent of the task

We already saw heightened STS and left PM activation, as being part of the action observation network, to a threatening situation independent of task. Seeing a threatening situation may prompt a reaction in the observer and trigger motor preparation (de Gelder *et al.*, 2004, Hoshi & Tanji, 2004). Another area involved in this is the hypothalamus. The hypothalamus has a direct connection to the brainstem and autonomic spinal centers, that can increase *i.e.* heart rate and breathing, all necessary to prepare the body for action (Barbas, 2003). In humans, electrical stimulation of the hypothalamus has been shown to evoke aggressive reactions (Bejjani *et al.*, 2002). These findings support the idea that the PM activation found here goes beyond mere action observation and reflects activity related to automatically triggered preparation for action in reaction to the threatening situation. Similarly, more responsiveness in bilateral putamen could be related to a higher motor response during threatening situations (de Gelder *et al.*, 2004).

The activation in hippocampus in relation to threatening situations is in line with previous research. In a study that used emotional and neutral faces whereby participants had to perform either an emotion or an age discrimination task, AMG and left hippocampus activation was found for the former task (Gur *et al.*, 2002).

One might argue that the differential activation between teasing and threatening movies reflects ambiguity inherent to the teasing situation possibly therefore requiring more decoding resources. However, the behavioral data do not support this since participants are equally accurate in explicitly judging the threatening and teasing movies. Furthermore, the threatening movies trigger activity in many areas, while for teasing ones only right SFG gets activated. This region has not been found in studies focusing on ambiguity (*e.g.* Nomura *et al.*, 2003, Hsu *et al.*, 2005, Jenkins & Mitchell, 2010, Winston *et al.*, 2003, Simmons *et al.*, 2006), where mostly medial PFC has been found.

■ Activation related to attending to the situation independent of the emotion

It may be the case that participants judge the situation they observe in the video on the basis of past experiences. This may explain the simultaneous activation of TP, PCC and mPFC which have been related to memory retrieval (Vincent *et al.*, 2006). These regions could work in tandem with frontal areas such as IFG and dmPFC to appraise the situation and extract the right information (Kober *et al.*, 2008). In the monkey, mPFC and OFC have, also via the AMG, strong connections going through the hypothalamus to the brainstem and efferent autonomic structures (Barbas, 2003). Possibly, the elevated activation here indicates a heightened state of alertness to be able to project information further into the spinal system once necessary.
But it could also be that dmPFC gets activated purely by paying attention to the social interaction. Namely, a study by (Iacoboni *et al.*, 2004) reported heightened activation in this region and in medial parietal areas when participants watched movies of everyday social interactions compared either to rest or to movies showing an individual in the same context. Also because these activities occurred together with activation in STS, IFG and FG, this led the authors to suggest that dmPFC and medial parietal areas are involved in the processing of social relations. Since we also found all of these regions activated – together with PCC – when participants had to focus on the meaning of the social interaction, our study seems to support this idea.

■ Activation related to inattentively observing an interaction independent of the emotion

When participants had to pay attention to the colored dots in the task in comparison with paying attention to the situation, we found more activation in regions within the occipital lobe which includes possibly area V4, an area important for color perception (Zeki *et al.*, 1991). Lesions in this area cause difficulty with allocating visual attention or it can result in achromatopsia (Zeki *et al.*, 1991, Gallant *et al.*, 2000). Since the movies were in black/white, searching for the dots was mainly searching for colors, therefore the finding that V4 was activated for this contrast seems very intuitive. Enhancement of these sensory features by attention might help in target detection.
Since the behavioral results show that participants performed the color naming task better than the emotion naming task, more activation in left precentral gyrus could be related to the certainty of the participants, leading to a stronger right button press for the former task.

Conclusion

We showed that right AMG is involved in witnessing threatening situations the observer is not part of, also when not actually paying attention to the situation. This AMG activation during the color naming task co-occurred with activations in body processing regions FG, EBA-hMT+/V5 and STS.

Regions involved in action perception (IFG and TPJ) responded more when the interaction was threatening and when attention was directed explicitly to it. Also left IPL showed a heightened response to threatening situations. Regions more related to motor preparation than action observation, left PM and putamen, were also shown to be more responsive for threatening than teasing movies.

As expected, regions involved in moral cognition (anterior TP, medial PFC, OFC and TPJ) were activated when an overt decision had to be made about the situation. But PFC and OFC were not activated more for threatening situations representing moral violations as one might have expected. However, TPJ and hypothalamus were activated in that condition.

In focusing on interactions, our study adds significantly to previous research using isolated faces or bodies. Taken together, our results show which regions are responsible for the ability of people to detect a situation they are not involved in themselves as a threat, and that they can do so even though they are not explicitly paying attention to the situation. Future studies need to focus on the timing of activation and the connectivity between the limbic system, body processing areas and higher cortical regions.

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Chapter 6

Perceiving threatening social interactions with different focuses of attention

"I have always thought the actions of men the best interpreters of their thoughts."
~ John Locke ~

Chapter based on:
Sinke, C.B.A., Goebel, R. & de Gelder, B. Perceiving threatening social interactions with different focuses of attention. (in preparation)

Abstract

Being able to recognize and react to a threatening social situation has considerable adaptive value and requires a rapid perception of the situation even if one's attention is occupied otherwise. Threat can come from another person and be directed towards the observer, but what is much less investigated is how we perceive incidental threat between two other people. Here we investigated how menacing interactions are perceived when focusing on one or the other protagonist, either the angry or the defensive one. Furthermore, we manipulated attention by having an easy vs. a difficult task.

Fifteen subjects were scanned using a blocked functional magnetic resonance imaging (fMRI) design while they were watching 1.5s movies (576 trials) of an interaction whereby one person threatens another. Subjects were instructed before each block to focus either on the left or on the right person to perform an easy or a hard color discrimination task. This involved spotting two dots (42ms) that appeared randomly on the attended body. In the easy task, the color differences were big and therefore easy to perceive. In the hard task, the color differences were small and therefore more attention was needed to be able to perceive whether they were of the same color or not. No explicit emotion judgment had to be made.

Behavioral results show that participants are most accurate and fastest when they perform the easy task on the angry person. With the easy task and attention directed to the defensive person, results show the highest speed-accuracy tradeoff. This indicates subjects put most effort here in performing well, probably because the angry person distracts them. In this condition we also observed the highest suppression in amygdala signal, possibly because of top-down cognitive control to ignore the threat. During performance of the hard task, it makes no difference on which person the attention is focused, so there is no observable overt attention switch. In left secondary somatosensory cortex an interaction between focus of attention and task difficulty was found; subjects seem to have less bodily response to the threatening social interaction when the hard task is on the defensive person. The network normally involved in processing social interactions was not modulated by the different conditions.

Introduction

Social interactions are very much part of our daily life. Often we observe interactions passively, while being involved in another activity and barely paying attention as our gaze moves from one to the other protagonist. As a matter of fact, very little is known about how we observe casual interactions and whether we preferentially attend to the most active cq. the aggressive or to the least active, cq. the victim. A number of

different factors may determine our attentional involvement. Some may be unrelated to the type of interaction we are witnessing, like when our gaze is directed to the color of the dress. Other factors are related to the interaction itself. For example, in case of an aggressive interaction, some people may focus on the aggressor and others on the victim. Also, do we feel differently about each, do we feel more empathy when looking at the attacked person or more threatened when looking at the angry one?

One study, which used movies of hand or feet in painful situations, showed that the presence of another person modulates the observer's brain activity to seeing the pain (Akitsuki & Decety, 2009). There was an increase observed in areas for social interaction and emotion regulation. Furthermore, left amygdala (AMG) showed a higher functional connectivity with other brain regions. This may signify increased alertness: when somebody is involved in inflicting pain to another, he might also be harmful to you. A recent magnetoencephalography (MEG) study showed point-light motion of two people boxing in an interactive way *vs.* independently. This difference modulated activity in bilateral occipitotemporal region already 300-400ms after stimulus onset (Hirai & Kakigi, 2009), suggesting a differential processing of the motion or the bodies. Also Centelles and colleagues (2011) used point-light displays of two characters mimicking more everyday social activities in either an interactive way or individually. Using fMRI, they found more areas active when comparing the social interactive *vs.* the individual, non-social, movements: areas involved in mentalizing (temporoparietal junction (TPJ), anterior superior temporal sulcus, dorsomedial prefrontal cortex) and action observation/execution (inferior frontal gyrus, premotor cortex (PM), intraparietal sulcus, superior parietal gyrus, and posterior STS (pSTS). Although pSTS has been found before to be responsive to action prediction violations (Pelphrey *et al.*, 2004), it did so more when the actions were performed by characters that looked much like humans, even though other, non-human like, characters showed the same biological motion pattern (Carter *et al.*, 2011). These results indicate that pSTS is involved in social processing more generally instead of just biological motion per se. Note that none of these studies explicitly instructed the participants which of the personages to attend to and there may be considerable individual variability in which person receives automatically more attention.

Facial or bodily emotions that signal threat (fear or anger) are more quickly processed and receive priority in the allocation of attentional resources (Lundqvist & Öhman, 2005). A structure that seems to play an important role in this reallocation of attention towards potential threat is the AMG. However, there still is a continuing debate about whether this structure processes threat automatically or only under low attentional load conditions. Many studies showed that there is a decline in AMG activation when task demands increase (*e.g.* Pessoa *et al.*, 2002, Bishop *et al.*, 2007, Lim *et al.*, 2008, Silvert *et al.*, 2007). More rare are studies showing AMG activation also under high attentional load (Williams *et al.*, 2005, Anderson *et al.*, 2003), where it is claimed

that it directs subjects' attention to potential threat. In that case it would seem to make sense that AMG responds more to threat located in the periphery than in foveal view, because it would be important for the organism's survival to relocate attention there. However, this idea has been challenged by a recent study (Morawetz *et al.*, 2010), where the AMG did not respond differentially to faces – being emotional or not – presented at different eccentricities.

We recently conducted a study on perception of whole body movements with fully realistic stimulus videos which extended our previous research on isolated faces or bodies. The goal was to find out whether the brain picks up subtle differences in body language of two persons in a social interaction that was either threatening or teasing (Sinke *et al.*, 2010). Seeing the exact same movies, participants either paid attention explicitly to the bodies (faces were blurred) to decide whether there was a threat or a tease going on or they performed a color discrimination task, depending on the task condition. For the latter task, three dots appeared randomly (for 40ms) somewhere on the bodies during each 3s movie. After each movie, participants had to indicate whether all dots were of the same color or not. We found that right AMG always showed more activity for the threatening than teasing interactions, together with areas involved in processing moral violations (TPJ, hypothalamus) and action preparation (PM, putamen). Interestingly, during the color discrimination task subjects performed better (*i.e.* showed higher accuracy) when the dots were shown during a threatening situation. Also then, the fusiform gyrus (FG) and STS showed higher activation, which suggest that the threat heightened the subjects' attention which made them perceive the bodies and therefore also the dots better.

In the present study, we used new interaction stimuli which also consisted of fully realistic interactions. We adapted our attention paradigm slightly in order to investigate the role of selective attention to one of the two actors. Instead of having the colored dots appearing on both bodies at the same time we used a spatial attention manipulation and placed the target dots only on one or the other protagonist. The interactions always involved an angry and a threatened, defensive person and there was no explicit emotion task this time. The dot manipulation ensured that participants paid attention to either the angry person or the defensive person. We also manipulated attentional load by using an easy or a hard target detection task while keeping the stimulus display constant. This way, we wanted to investigate a possible difference in processing an interaction in which one person is angry at the other when focusing on just one or the other.

We expected that focusing on the angry as opposed to the defensive person would give rise to more activation in areas related to processing threat, like AMG and PM, and body shape processing areas like extrastriate body area (EBA) and pSTS. Secondly, we were interested in whether there is a difference in processing when less attention is available due to higher task demands. Is the social network differently activated? Does the brain still process the threat? We expect that the AMG will show more activation

when focusing on the angry than defensive person, but only during the low load condition.

We decided to use only male actors and male participants to rule out the impact of gender. In a recent study it was found that male participants responded most strongly to threatening male actors (Kret *et al.*, 2011). Also, it has been found that AMG responds more in males to negative affect (Schneider *et al.*, 2000) and men relative to women have a greater absolute metabolism during resting state in this area (Gur *et al.*, 1995).

Methods

■ Participants

Fourteen healthy volunteers (all male; 23.6 ± 4.1 years; all right-handed) participated in this experiment after providing written informed consent. All participants had normal or corrected-to-normal vision and were not color-blind. The study was performed in accordance to the *Declaration of Helsinki* and was approved by the local medical ethical committee. One subject was excluded from fMRI analysis because of excessive head movement.

■ Materials

Twelve actors (six male) were filmed while they were engaged into a social interaction which always involved two persons of the same gender. One of the actors spoke angrily towards the other person who reacted spontaneously and in a defensive manner. Only the movies of the male actors were used.

The raw footage was edited into 1.5s movies (720 x 576 pixels; 25 frames/second; 780kbps data rate; 24 bit sample size; compressed by Indeo video 5; 11 x 16.5 cm on screen) using Ulead VideoStudio (version 10) and processed with Adobe After Effects (version 6). Editing comprised blurring of the faces, removing sound and, in a later stage, converting the videos into black/white and putting a colored dot randomly on one of the bodies (above the knees) in two frames (for 40ms, visual angle = 0.26˚) of each movie. Eight different colors were used (red, pink, purple, blue, turquoise, green, yellow, and orange) and the dots per movie could be of the same or different color. For the easy task, the different colors in a movie diverged much in hue so the difference was undemanding to see (*e.g.* blue and yellow). On the other hand, the different colors in a movie from the hard task differed little in hue (*e.g.* blue and purple) which therefore needed more attention to spot. All colors appeared as often in all conditions. All movies were also mirror-reversed.

First, all movies without dots were validated for emotional significance by a group of participants using VAS-scales. For each movie, they had to indicate both how threatening and how realistic they perceived the interaction to be. Twelve movies per

actor combination that were perceived as most threatening and realistic were selected. Each individual movie was used for each condition.

Those movies including the dots were validated for task by a different group of participants (n= 16). The easy task was indeed easier than the hard task as shown by the accuracy rates (easy: M = 90.7%, SD = 6.52; hard: M = 74.0%, SD = 8.58) and a repeated measures univariate analysis of variance (ANOVA) with two factors (person - task) and two levels (angry/defensive - easy/hard) ($F(1,15) = 66.652$, $p = .000$, $\eta_{p2} = .816$). Participants were also faster for the easy than the hard task as shown by the reaction times ($F(1,15) = 25.726$, $p = .000$, $\eta_{p2} = .632$).

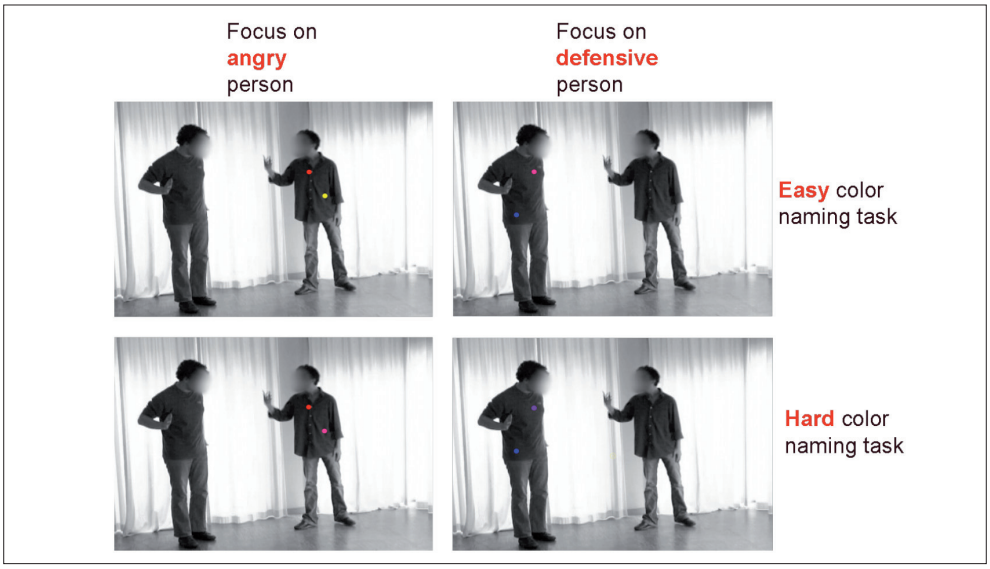

Figure 1. *Design of the fMRI study. 2x2 factorial design; 1.5s movies of one man guy being angry at another, being the same in all conditions. Overlaid on either the angry or defensive guy is an easy or hard dot color naming task.*

■ Design and procedure

A blocked fMRI design (see Figure 1) was used to ensure participants deployed the right attentional resources. In one stimulus block, nine stimuli were presented with an interstimulus interval (blank screen) of 1167ms. Every session comprised 4 runs of 16 stimulus blocks of 24s and 17 fixation blocks of 14s, with an anatomical scan in the middle. Each stimulus block was preceded by an instruction screen of 1500ms which indicated by showing a big or small circle at the left or right side of the screen whether the task was easy or hard and whether the dots appeared on the left or right person. Participants were instructed to try to ignore what happened in the interaction and press as fast and accurately as possible whenever they perceived the second dot whether it's color was the same or different from the first one (buttons randomly reversed per

participant). Also they were told to always press once for each movie, also in case they had not perceived a dot, so there was always a motor response for each movie. They first had some practice trials outside the scanner at the beginning of the session to get familiarized with the task, the instruction screen and all possible colors. Over the session, a total of 576 trials were presented. All originally oriented and all mirrored movies were shown in separate runs.

At the end of the scanning session, a localizer run for the perception of faces, bodies, houses and tools was given. This run included five 12s blocks of each stimulus category, interleaved with 14s fixation blocks. In one stimulus block twelve stimuli were presented for 450ms with an inter stimulus interval of 600ms. Here, subjects had to perform a one-back task.

Stimuli were presented using Presentation software (Neurobehavioral Systems, Inc, version 11.0) onto a screen located at the end of the scanner bore (at the side of the participants' head) with a liquid crystal display (LCD) projector (PLC-XT11-16, Sanyo North America Corporation, San Diego, USA). The participants viewed the stimuli via a mirror mounted to the head coil at an angle of ± 45°.

■ fMRI data acquisition

The MRI unit used was a commercial head scanner with a magnetic field strength of 3T (Siemens Allegra, AG, Erlangen, Germany) provided with an eight-channel head coil. Foam padding placed around the head was used to minimize movement and the participants were provided with ear plugs to reduce the scanner noise.

In each session, after a first quick nine-slice localizer for orientation, a three-dimensional (3D) T1-weighted data set was scanned using parameters from the Alzheimer's Disease Neuroimaging Initiative (ADNI) encompassing the whole brain (scan parameters: repetition time (TR) = 2250ms, echo time (TE) = 2.6ms, flip angle (FA) = 9°, field of view (FOV) = 256 × 256mm^2, matrix size = 256 × 256, number of slices = 192, slice thickness = 1mm, no gap, total scan time = 8m and 26s).

The scan parameters for the functional run were: TR = 2000ms, TE = 30ms, FA = 90°, base resolution = 64, FOV = 224 × 224mm^2, 32 interleaved slices of 3.5mm (no gap), number of volumes = 326 per run (scan time = 10m and 52s). Total scan time per session was 61min.

The scan parameters for the localizer run were: TR = 2000ms, TE = 30ms, FA = 90°, base resolution = 112, FOV = 224 × 224mm^2, 28 interleaved slices of 2mm (no gap), number of volumes = 267 (scan time = 8m and 54s).

■ Behavioral data analysis

Trials were removed in which the response time (RT) was below 200ms, above 1200ms or exceeded the individual mean RT by more than two standard deviations. Inverse efficiency scores (IES) were calculated by dividing the mean RT per condition

per subject by the mean accuracy rate for that condition. This was done in order to discount for possible speed-accuracy tradeoffs in performance. To test whether performance (error rate, correct RT and IES) on the color naming tasks was influenced by whether attention was on the angry vs. the defensive person, a repeated measures univariate analysis of variance (ANOVA) was performed in SPSS (version 15.0 for Windows) with two factors (person - task) and two levels (angry/defensive - easy/hard). One subject had to be excluded from analysis because of missing RT data.

■ FMRI data analysis

For the fMRI data analysis BrainVoyager QX (version 1.10 Brain Innovation, Maastricht, the Netherlands) was used. A number of preprocessing steps were performed on the functional data. These included incremental linear trend removal to eliminate scanner-related signal drifts; temporal high-pass filtering to remove temporal frequencies lower than 3 cycles per run; and a rigid body algorithm which rotates and translates each functional volume in 3D space in order to correct for small head movements in between scans. For the group ANOVA, the data was spatially smoothed with a 4mm Gaussian kernel. To enable the comparison between participants, all anatomical as well as functional volumes were spatially normalized into Talairach space. The first two scans per run were excluded from the analysis to permit T1 equilibration effects. The 3D T1-weighted scans were used to overlay the statistical maps on for anatomical orientation.
At single-subject level, fixed-effects whole brain ANOVAs were performed using a regression model consisting of the five predictors corresponding to the particular experimental conditions (the two task conditions on the angry and the defensive person plus a fifth for the instruction screen). The predictor time courses used were generated on the basis of a linear model of the relation between neural activation and hemodynamic response. Furthermore, regions of interest (ROIs: EBA and FBA) were localized by contrasting all bodily stimuli versus the faces, houses and tools. Most were chosen with at least FDR correction. However, for some the threshold was set a bit lower to get a cluster of at least 50 voxels. For the AMG a mask was used. Beta-values from the ROIs were extracted from BrainVoyager into SPSS (Version 15.0) in order to perform a random effects ANOVA to look for interaction effects and main effects of person and task. In case of an interaction, paired-samples t-tests were performed to look specifically at both tasks and both persons separately and to see whether the conditions differed from baseline.
At group level, a single subject ROI-based group ANOVA with two within-subjects factors (person x task) with two levels (angry/defensive – easy /hard) was performed. Secondly, a whole brain random effects ANOVA with the same factors was performed to exploratory look for the main effects of emotion and task and for interaction effects. The resulting volume maps per contrast were subjected to a cluster-level statistical threshold analysis in order to correct for multiple comparisons (Forman *et al.*, 1995, Goebel *et al.*, 2006). For the analyses within the ROIs, a threshold of $p < .05$ was used.

The whole brain analyses were corrected for cluster-size. Only the group results are reported. Additionally, we looked for correlation between RTs and brain activation for all the separate conditions.

Results

■ Behavioral results

The accuracy rates confirm the difference between the easy and the hard task ($F(1,13) = 86.067$, $p = .000$, $\eta_{p2} = .869$). There was almost an interaction ($F(1,13) = 4.658$, $p = .050$, $\eta_{p2} = .264$). Paired-samples t-tests showed that in the easy condition, participants performed better when the dots appeared on the angry person ($t(13) = 2.599$, $p = .022$, $d = .575$).

Reaction times showed an interaction ($F(1,13) = 151.154$, $p = .000$, $\eta_{p2} = .921$), main effect of person ($F(1,13) = 67.559$, $p = .000$, $\eta_{p2} = .839$) (faster when dots are on angry than defensive person) and main effect of task ($F(1,13) = 47.228$, $p = .000$, $\eta_{p2} = .784$) (faster for easy than hard task). When dots are on the angry person, participants are faster during the easy task ($t(13) = 11.316$, $p = .000$, $d = 1.045$) and during the easy task subjects are faster when dots are on the angry than defensive person ($t(13) = 11.605$, $p = .000$, $d = .974$).

Inverse efficiency scores also showed an interaction ($F(1,13) = 32.647$, $p = .000$, $\eta_{p2} = .715$), main effect of person ($F(1,13) = 33.020$, $p = .000$, $\eta_{p2} = .718$) (faster when dots are on angry than defensive person) and main effect of task ($F(1,13) = 162.759$, $p = .000$, $\eta_{p2} = .926$) (faster for easy than hard task). Performance was worse for both hard task on angry person ($t(13) = 12.493$, $p = .000$, $d = 2.529$) and easy task on defensive person ($t(13) = 9.248$, $p = .000$, $d = .976$) than easy task on angry person. Performance on easy task on defensive person was better than hard task on this same person ($t(13) = 9.183$, $p = .000$, $d = 1.390$). See Figure 2.

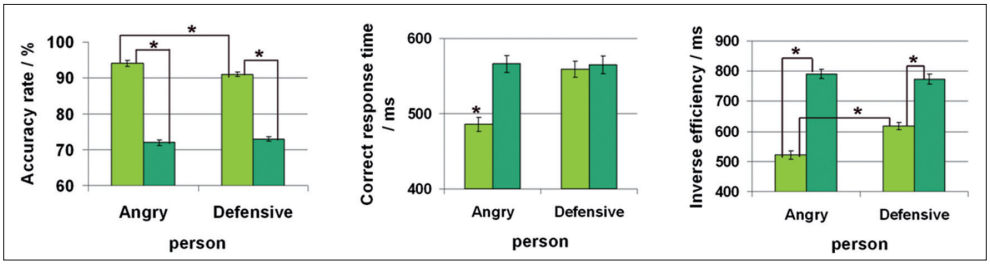

Figure 2. *Behavioral results. Mean accuracy rates, correct response time (RT) and inverse efficiency scores (IES) for the easy (light green bars) and hard (dark green bars) color naming task on the angry and defensive person.*

■ fMRI results

ROI analysis

The body processing areas in the left hemisphere did not show any effects. Right EBA showed only a trend for being more responsive during the easy than hard task ($F(1,13) = 2.472$, $p = .140$, $\eta_{p2} = .160$) and during looking at angry than defensive person ($F(1,13) = 3.293$, $p = .093$, $\eta_{p2} = .202$). The latter effect was significant in right FBA ($F(1,13) = 5.665$, $p = .033$, $\eta_{p2} = .304$) but being more responsive during the easy than hard task was also here only a trend ($F(1,13) = 3.307$, $p = .092$, $\eta_{p2} = .203$).
Left AMG showed a trend towards an interaction ($F(1,13) = 4.560$, $p = .052$, $\eta_{p2} = .260$) and was more responsive when looking at the angry than defensive person ($F(1,13) = 5.017$, $p = .043$, $\eta_{p2} = .278$), especially during the easy task ($t(13) = 2.709$, $p = .018$, $d = .45$). See Figure 3. Right AMG did not show any differences in response to all conditions.

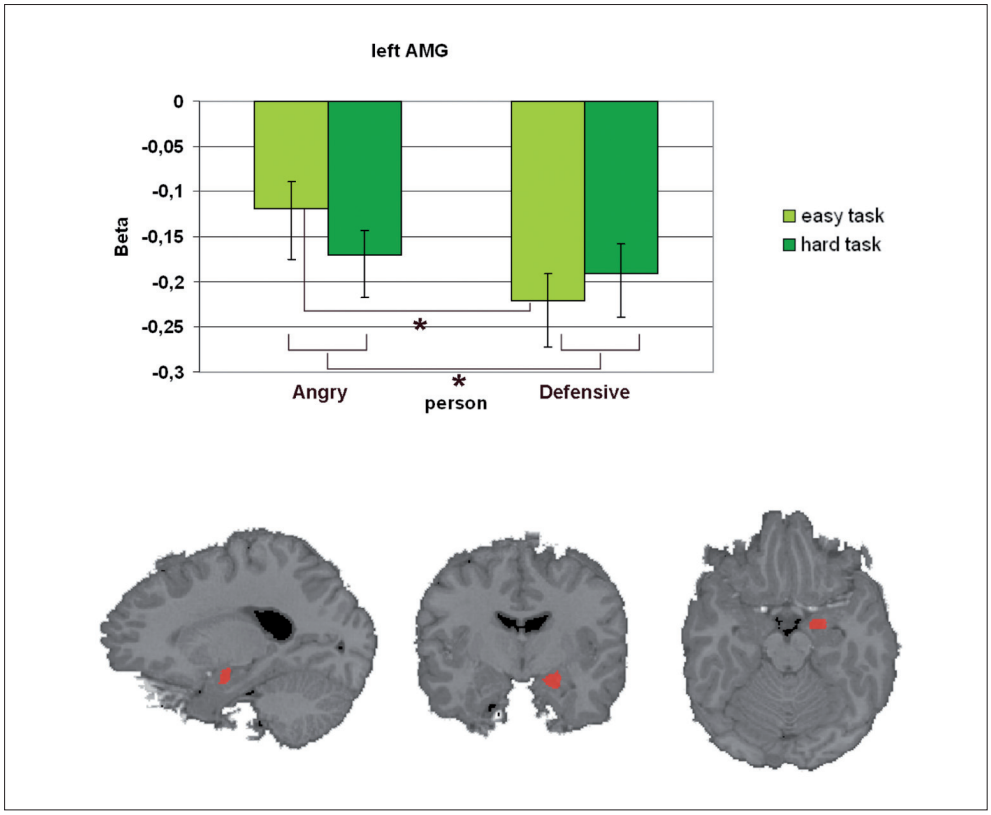

Figure 3. *Region-of-interest (ROI)-based group analysis in left amygdala (Tal x,y,z(-19,-7,-13)). It shows a main effect of person (angry > defensive) and there is a trend for an interaction (p<.052), showing more activation for the angry easy than defensive easy condition.*

Whole brain analysis

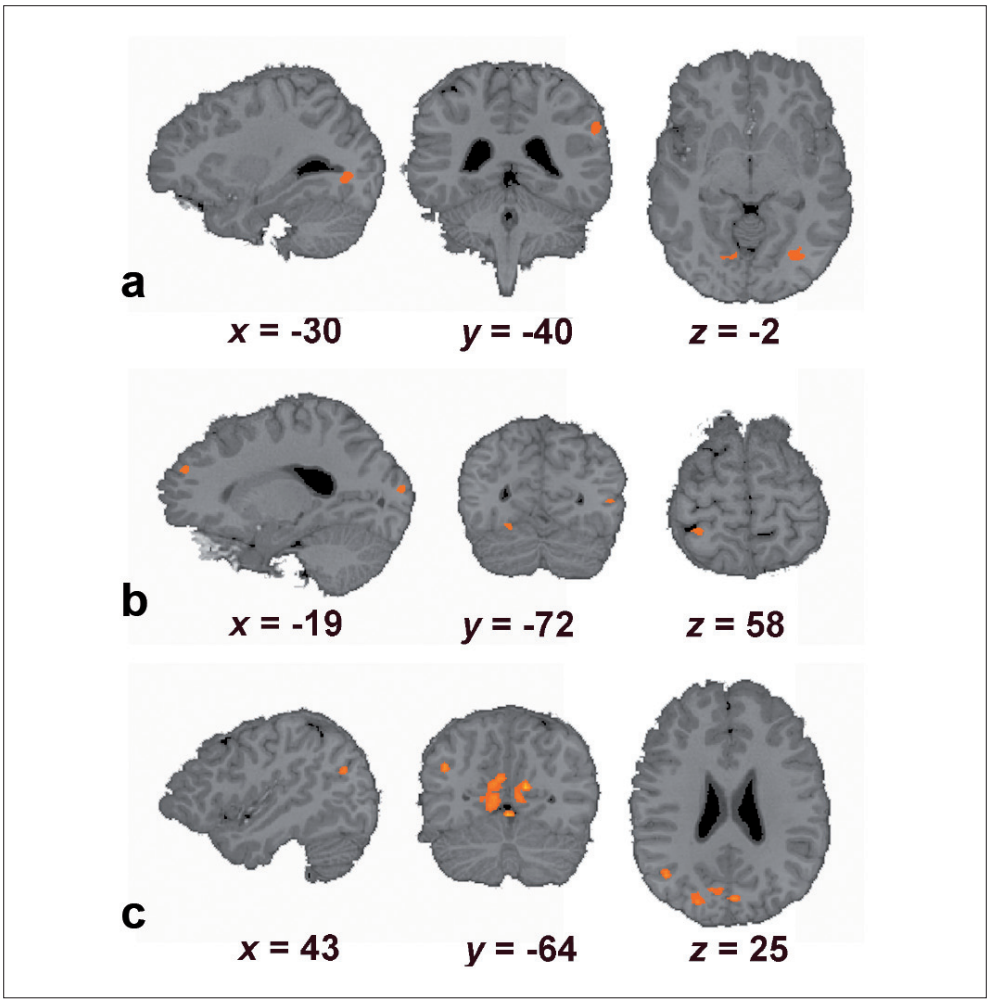

Figure 4. *Group results of whole brain ANOVA (p<.001; neurological convention). (a) Interaction: left SMG, left collateral sulcus, right MOTG. (b) Main effects focus of attention (angry > defensive): MOG, right MOTG, left collateral sulcus, right SPL, left SFS, left ACC. (c) Main effects task difficulty (easy > hard): right IPL, cuneus.*

Table 1. *Interaction and main effects between focus of attention and task difficulty as found with whole brain ANOVA ($p < .001$, cluster-size corrected).*

Region (Broca's Area)	*Hemisphere*	*x*	*y*	*z*
Interaction:				
Supramarginal gyrus (40)	L	-57	-40	32
Collateral sulcus (18)	L	-32	-72	1
Middle occipito-temporal gyrus (19)	R	9	-67	-2
Angry > defensive:				
Middle occipital gyrus (18)	L	-44	-68	5
Middle occipital gyrus (18)	R	45	-62	3
Collateral sulcus (18)	L	-5	-94	5
Middle occipito-temporal gyrus (19)	R	18	-78	-9
Middle occipital gyrus (17)	L	-21	-92	13
Middle occipital gyrus (17)	R	22	-89	7
Superior parietal lobe (7)	R	35	-42	60
Superior frontal sulcus (10)	L	-18	52	27
Anterior cingulate sulcus	L	-6	33	13
Easy > hard:				
Inferior parietal lobe (19)	R	42	-63	27
Cuneus (18)	Bilateral	7	-72	15

Regions showing an interaction between person and task

An interaction between person and task was found in right middle occipitotemporal gyrus (MOTG), left supramarginal gyrus (SMG) and left collateral sulcus. The former two showed least activity for the defensive hard condition. In collateral sulcus there was more activation for angry than defensive during the hard task while more activation for defensive than angry during the easy task. Also, here was more activation during easy than hard when the task required attending to the defensive person. See Figure 5. The activity in SMG showed a positive correlation with all RTs and IESs.

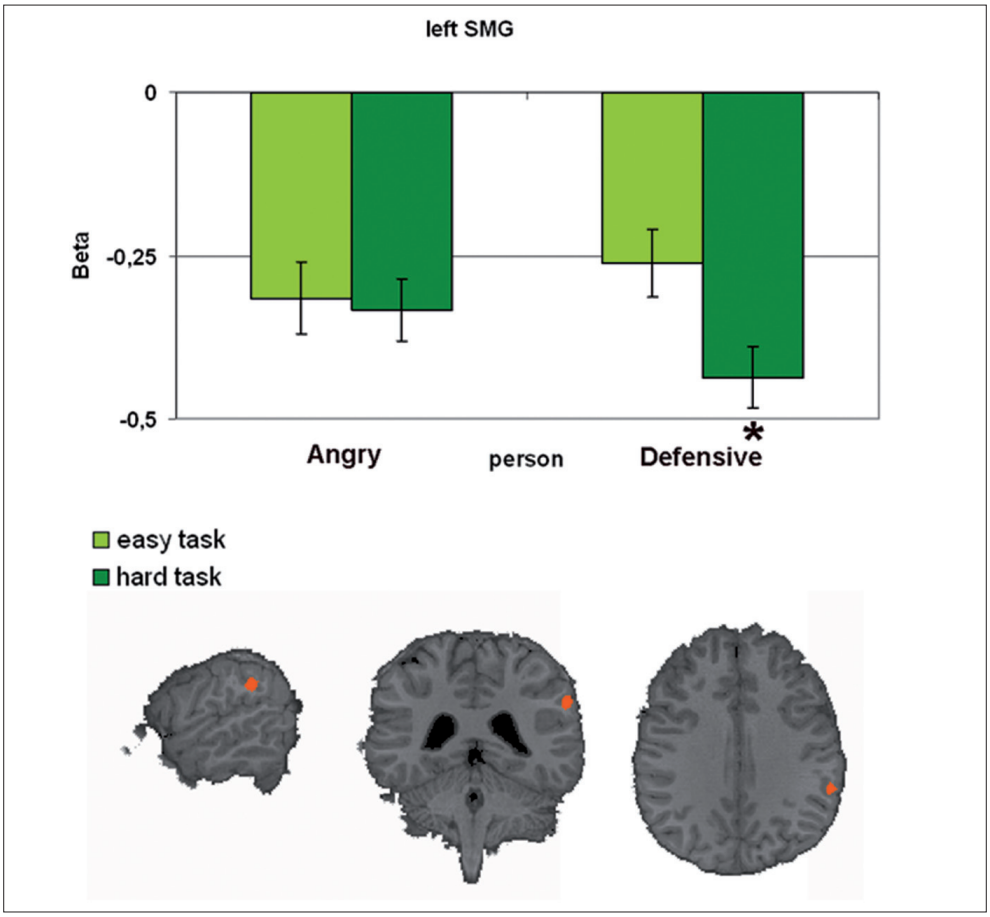

Figure 5. *Interaction in supramarginal gyrus (SMG) as found with a whole brain ANOVA (p<.001, cluster-size corrected; neurological convention; Tal x,y,z(-57,-40,33)). The hard defensive condition shows least activation compared to the other conditions.*

Discussion

Our goal was to find out how observers perceive a threatening social interaction and to compare the activation pattern for the situation of attending to the aggressor *vs.* attending to the victim. Participants performed a color naming task and we manipulated level of difficulty in order to measure the effect of task load on fear triggered by seeing the aggression *vs.* empathy triggered by seeing the victim.
The behavioral data show that participants perform better and faster during the easy than hard task, which supports a correct implementation of task difficulty. During the hard task, there is no difference between focusing on one or the other person in

accuracy, RT and IES scores. However, during the easy task subjects are better, faster and have overall better recognition when the task is on the angry person.
In our previous experiment, participants also performed better (no RT was measured) during threatening situations than during teasing ones although in this case their attention was on the whole scene. So the present results are consistent with our previous study in showing that performing a task that involves processing a task irrelevant threatening stimulus, being in the focus of your attention, improves task performance.
Concerning the RTs, when we look at a similar study by Pichon *et al.* (2011) in which dynamic single body stimuli were used, subjects are actually slower when the dot task appears on an angry than neutral person (Pichon *et al.*, 2011). Similarly, in the emotional Stroop task, subjects are slower in naming the color of a threatening than a neutral word because the threat captures their attention, which slows down the color naming (Watts *et al.*, 1986). However, in these studies the threat condition is always compared with a separately presented neutral word or person while in the present study there are in fact two stimuli at the same time, one of which is always threatening. In the same vein as the Stroop task, subjects are indeed distracted by the threat when the task is on the defensive person, which makes them respond slowly. When the task is on the angry, threatening person, subjects might just as well be distracted but not that much since their attention is already on the right spatial location so no attention shift is needed.
This gets clear when we look at the IES. The easy defensive condition shows a shift from the RT. Apparently in this condition, subjects trade time for accuracy. This supports the idea that they are distracted here by the angry person while focusing on the defensive one, with the consequence that they do need more time to respond. This distraction by the angry person however, is only clear in the easy task condition. During the hard condition, there is no difference between focusing on the angry or defensive person for all behavioral measures. It seems that in this case, there are not enough attentional resources left to process the threat which would be consistent with attentional load theory, stating that interference from irrelevant distracters only happens under conditions of low perceptual load (Lavie, 1995). Threat is often seen as a special case because of its evolutionary significance, which makes it in this way a relevant distracter. Processing of threat is often found to occur automatically (Öhman *et al.*, 2001) and even outside awareness (Esteves *et al.*, 1994). Anderson *et al.* (2003) found that the threat is not fully automatically processed; only the AMG did not respond differentially when subjects watched fearful (but not disgust) faces. But more studies found also the AMG responding differentially to fearful faces (Silvert *et al.*, 2007; Morawetz *et al.*, 2010; Bishop *et al.*, 2007).
In the present study, left AMG showed more activation when focusing on the angry than defensive person. To a certain extent, it would be useful in the former condition that the threat heightens your attention because this will probably also make you perceive

the dots better that appear on the body. However, when you are focused on the other person, you do not want to be distracted by the angry person which would lead to an automatic (covert) attention shift which makes it harder for you to perform the task. In order to keep performing well, you will have to try to suppress the distraction from the threat. This effort can be related to the speed-accuracy tradeoff we see in the IES for this condition, and to the found deactivation in AMG in the angry easy condition. Becker and Detweiler-Bedell (2009) failed to find an overt attentional bias towards fearful or angry facial expressions; their subjects actually actively avoided looking at them (Becker and Detweiler-Bedell, 2009). So this actively avoiding might need some cognitive resources which take more time. Such deactivation of the AMG has been found in emotion studies that involved increased cognitive demands by active attentional processing (Drevets and Raichle, 1998; Costafreda, 2008). For example, in a recent study whereby at the same time emotional faces and letters or digits were presented, AMG showed a deactivation that was more pronounced in the ignore faces than attend faces condition (Morawitz *et al.*, 2010). Pessoa and Ungerleider (2004) reported that in the presence of a highly demanding, non-emotional task, the presentation of emotional faces was not associated with AMG activation (Pessoa and Ungerleider, 2004). Furthermore, AMG gets mostly activated by emotional faces (Costafreda, 2008), which were not visible here.

A strong interaction was found in left SMG (Broca's Area 40) which is part of secondary somatosensory area (SII), implicated in pain and visceral sensation (Eickhoff *et al.*, 2003) and body state representations (Damasio, 2003). It responds less to the defensive hard condition than to all other conditions. This could mean that for this condition, subjects have less bodily feeling with the social interaction. Within this area, an interplay between cognition and emotion could take place. Together with AMG and posterior middle frontal gyrus, it seems to be involved in effortful coping with emotional distracters when a controlled response is required (Wang *et al.*, 2008). This makes sense here: During the hard defensive condition, most effort is needed not to mingle cognition and emotion; namely to suppress an attention switch to the angry person plus heightened attention to be able to see the color differences at all. Interestingly, its activity here is positively correlated with both the individual RTs and IES. So the higher the RT and IES were, the more activity there was in SMG. Its signal was found to be modulated by AMG (Adolphs & Spezio, 2006), but we did not observe a correlation between those two activation levels here. Specifically in the left hemisphere has SMG been associated with the storage of phonological information and verbal working memory (Smith & Jonides, 1999), so its activation here could also be related to keeping the first colored dot in working memory for subsequent comparison with the secondly presented one.

The focus of attention seems to have more effect than the task difficulty on brain activation. The MOG clusters overlap with what could be EBA. In that case, there is an emotional modulation as found in previous studies. However, we did not find this

same result in the functionally localized EBA. Only in right FBA we found in this way a higher response when focusing on the angry than defensive person.
Some areas that were found before for processing social interactions, like TPJ, precuneus and temporal pole, were not found in this study. This probably means that the areas cq. networks processing interaction are not differentially sensitive to whether you focus at the angry or defensive person and whether you perform the easy or hard task.

Conclusion

We argue that during low task level performance, subjects are mostly distracted by an angry person, leading to a higher suppression effort when focusing on another spatial location – the defensive person – to be able to perform the task at a similar level as when focusing on the angry person. This was shown by the lowest activation in AMG and the biggest speed-accuracy tradeoff for the easy defensive condition. However, during the easy task, subjects perform better when focusing on the angry person because it probably heightens their attention. In SMG – SII – an interaction was found between focus of attention and task difficulty; subjects possibly have least bodily feelings to the social interaction when focusing on the defensive person during the hard task condition. Whether you focus on one or the other person does not influence the processing in the network normally involved in social interactions.

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Chapter 7

Summary and general discussion

"If we knew what we were doing, it wouldn't be called research"
~ Albert Einstein ~

Hardly any day goes by for us without having contact with other people, whether it is in real life or over the phone or the internet. Since we are such social beings, we have become real experts in guessing other people's feelings even when they try to hide their true intentions. This is made possible by specialized brain mechanisms that have evolved over the course of time.

The work described in the previous chapters had several goals. One of them was to look into cultural differences in recognizing facial and bodily expressions and whether the social context has a different influence on this recognition. Another intention was to see whether the emotion from the context has an influence on face processing in the brain. A final aim was to explore whether threat can be recognized from dynamic body language alone, even though the threat is not directed towards the observer and even though the observer has his mind on something else.

In Chapter 2, behavioral results showed that there are indeed cultural differences between Dutch and Chinese students in how Caucasian facial and bodily expressions are recognized. Chinese had worse recognition memory for neutral faces than Dutch, but once emotions were involved they were just as good. Whether this is the case because emotions helped better storage of the faces or better recollection cannot be said. It does show that emotions have a special connotation. For several match-to-sample tasks, Chinese were slower than the Dutch students, with exception for the face identity tasks. For these faces, Chinese were faster and more accurate. This is an interesting result since Asian countries are more collectivistic – as opposed to individualistic western countries – and people are more conforming to the group. This means they try to hide their personal ideas and intentions more often which might have led to their expertise in looking at faces in order to deduce people's true intentions. When emotions were involved, Chinese performed as accurate as the Dutch, although slower. Also, when having to judge bodily emotions in a non-social context, Chinese needed more time to do so. Only when the bodies were presented in a social context, Chinese were actually faster, and at the same time more accurate. It seems like the social surrounding had given them an incentive to perform faster and better, which can be related again to their collectivistic society.

Chapter 3 showed that fearful faces lead to more activation in fusiform gyrus when the scene they are presented in is also fearful. This was expected to be the case as well for neutral faces as found in previous electroencephalographic research. However, this was not found here. But of course it is difficult to compare results found by different brain imaging methods since they measure different processes. Place processing areas in the brain responded less to scenes when the scene was threatening and also when a face was presented in it. So both facial and emotion processing seem to decrease scene processing, indicating the importance of the former two over the latter.

Chapter 4, elaborating on the previous chapter, showed that extrastriate body area (EBA) responds to threatening scenes, even though no body is presented within it. Whether this is due to imagination of people fleeing from the scene or to own bodily

feelings in response to the stimulus is open to debate. However, it shows that EBA's function is not that clear-cut yet.

Moving on from static pictures of single faces or bodies to dynamic stimuli of two people interacting, it was shown in Chapter 5 that the brain responds to threatening situations even when attention of the observer is on an unrelated task. Areas responding here were limbic areas like amygdala (AMG), hypothalamus and hippocampus but also putamen and premotor cortex that are involved in action observation and preparation. These results illustrate the important action component of emotion. Subjects performed the unrelated task actually better when the situation was threatening. In this case, body processing areas in the fusiform gyrus and superior temporal sulcus also responded more to the threatening than teasing interactions. The AMG seems to play a big role in this process. There has been much debate in the literature on whether AMG responds to threat automatically. In this study it does, even though the threat is not directed towards the observer. This study also is in line with previous studies on mentalizing, since similar brain regions – including anterior temporal pole, medial prefrontal cortex, orbitofrontal cortex, and temporoparietal junction – were activated during active judgment of the actors' intentions by the subjects.

Continuing on the importance of recognizing threatening stimuli, in Chapter 6 it is described that focusing on an angry person in a social interaction helped subjects to perform better on an unrelated task. On the other hand, the angry person distracted them when they performed the same task on the other, defensive person. However, this was only the case when there were enough attentional resources left. When focusing on a different spatial location and at the same time performing a high attentional load task, the threat did not have an influence on behavior anymore. Also, AMG responded more when focusing on the angry than defensive person during the easy task condition. So there seems to be a limit in how automatically AMG responds to threat, and attention seems to play a role in this. Observers possibly have least bodily feelings to the threatening social interaction when focusing on the defensive person and having not enough attentional resources left as implicated by the found interaction in secondary somatosensory area.

Taken together, these studies show that emotions have a special influence on brain processes; they help overcome the recognition memory disadvantage for other-race faces; expressed in the body by Caucasians they are as accurately recognized by people from an Asian as from a western culture; expressed in a scene they have an influence on face processing; and expressed in a body they have an influence on our behavior even though we are occupied with other affairs and even though they are not directed towards ourselves – at least to a certain extent.

■ Emotions are a means of communication

In everyday communication we normally always focus on people's faces. We get extra information by noticing small changes in facial muscle tensions when listening to

what someone is saying. However, we also pick up changes in body movements, even though most people are unaware of this. Because of this unawareness, people try to control only their facial expression when lying (Ekman, 2003). However, this thesis shows that body movements can also give us a lot of information and have an influence on our behavior, even though we are not specifically focused on extracting this.

Still, humans are quite experienced in face processing. In Chapter 3 it was shown that face processing seems to receive priority over scene processing; once a face is presented in a scene, the place processing areas are less activated. On the other hand, face processing areas are not less activated when they are presented in a scene. It is as if faces receive most attention. Even when the scenes were threatening, the place processing areas responded less when a face was presented simultaneously within the scene.

Even more so, in contrast to faces and bodies that give rise to more response in the face and body processing areas once they express fear, scene processing in place processing areas is decreased once there is a threat within the scene itself. So emotion seems to be not directly linked in the brain to scenes but more so to biological stimuli. However, in this study, the nonsocial context affects fearful face processing when it shows a threat. This might indicate that when there is already a biological incentive for threat, a non-social threat can heighten the attention and by doing so increase face, and probably also body, processing.

Indeed, we found EBA getting activated for threatening scenes even though no body was present in the stimuli as described in Chapter 4. Apparently, when there is a threatening scene, more happens in the brain than just basic processing what is perceived.

So emotions have a special influence. They take away attention from scene processing and they improve face and body processing. Also, they can help overcome the other-race recognition memory disadvantage as shown in Chapter 2. It is as if they make faces more salient and therefore better to remember.

■ Emotions imply actions

When we experience an emotion, it is normally accompanied by a motivation to do something. Those action tendencies are what actually define emotions (Frijda, 1986). An exception might be sadness, an emotion which normally generates passiveness. This is the only emotion where no action is involved. Maybe because it is very distinct from the other emotions in this way, this expression was perfectly recognized in the body by both Chinese and Dutch students as found in Chapter 2.

Also perceiving emotions in others, can lead to action tendencies in ourselves. Some believe this is due to mirror neurons. These are neurons that were found in the premotor cortex of macaques that are activated when we observe someone performing a movement as well as when we perform the same movement ourselves

(Gallese *et al.*, 1996). This way supposedly, we can understand the actions of others. Some people discuss about the role these neurons might play in empathy.
Either way, there is no doubt that perceiving emotions in others does have a direct influence on us. We saw in Chapter 5 and 6 that the perceived threatening emotions have an influence on behavior. When the focus was on the emotion, it made subjects perform better on an unrelated task. When the focus was on a different spatial location than where the threatening body language was shown, the performance on the unrelated task declined, although only during an easy task.

■ Emotions suggest motion

A persistent critique from people outside the area of emotion research is that findings about perception of emotional body actions may only reflect motion and not emotion perception. However, motion is inherent to emotion. Angry involves generally very active movements, while sadness on the other hand is very passive. Motion is very powerful; observing a static picture of someone in action can already activate the human motion area (hMT+/V5). Bodies normally always accompany movements, making it logic that EBA lies very close to hMT+/V5. In Chapter 4 where we found EBA getting activated for threatening scenes, we were indeed sure it was EBA and not hMT+/V5. This was because we had the opportunity to functionally localize this body area post hoc per subject, which showed the overlap with the found activation. But even though, whether the activation presented here was due to bodily representation or movement, it does mean that the stimuli lead to more brain activation than merely the visual processing of it.

■ Emotions and context

Many different factors can have an influence on how we perceive emotions. Perceiving a surprised face as happy or sad can depend on verbal information (Kim *et al.*, 2004). You might respond in a different manner to emotions depending on your age; adolescents showed a greater response to fearful faces in AMG and FG than adults (Guyer *et al.*, 2008). Also gender can have an influence; males tended to show more brain activity to threatening male body expressions as opposed to threatening female body expressions than females do (Kret *et al.*, 2011). Expectations and past experiences also play a role; when walking through a dark park or when you have been attacked once, you are probably more at guard and therefore might make you perceive a social interaction sooner as threatening as you would when perceiving the exact same situation during daylight in a friendly neighborhood. People that have high anxiety levels probably respond differently to threatening stimuli than others. Studies showed that there is a relationship between recognition of facial expressions and behavior problems involving aggression (Blair, 2003). And not only disorders, also just a change of mood could have an influence on emotion perception.

Even though Darwin believed that many basic facial expressions are similar across cultures, emotions can be perceived differently in different cultural contexts. First of all, there can be clear different facial features like skin color that immediately tell us people do not belong to the same racial group as us, which make us respond differently to them. Infants of only three months old already show a preference for own-race faces (Kelly *et al.*, 2007). When observing fearful Japanese or Korean versus Caucasian faces, the AMG responds more to the same-race faces (Chiao *et al.*, 2008; Lee *et al.*, 2008). Also, because of different values and norms we have grown up with, people from different societies might be more or less expressive in their emotions. This can also have an effect on which part of the face people from different cultures mainly focus (Yuki *et al.*, 2007). When having to infer mental states from the eye region of Caucasian and Japanese faces, subjects performed better for stimuli of their own culture. Also, different brain areas got activated for doing this for the same or for the other culture (Adams *et al.*, 2009).

■ Emotions and attention

Emotion and attention are highly related. Emotional faces capture attention (Vuilleumier & Schwartz, 2001) and emotions - by receiving more attention - can lead to a higher activation in face and body processing areas (as shown in Chapter 3 and 5), which suggests a better representation of the faces and bodies. This seems to be driven by the AMG, a structure that responds to highly salient events and directs attention towards them. There seems to be a feedback mechanism from AMG to FG that enhances visual processing of faces (Breiter et al., 1996). In Chapter 5 it was found that during unattended threatening interactions AMG responded more to the threat, as did FG and STS. So it seems very plausible that the same mechanism as for emotional faces is at work for dynamic bodily expressions.

Whether the AMG is able to respond to emotional events independent of attention, has been a matter of debate for some time now as discussed in this thesis before. In Chapter 5, the AMG responded to the threatening social interaction, independently of whether subjects explicitly paid attention to the situation or focused on an unrelated task. In Chapter 6 the AMG did also show more activation when focusing on the angry than defensive person. However, there was also a very high trend for an interaction which would probably become clear when having scanned some more subjects; more activation when focusing on angry than defensive person only during the easy task. This nicely fits with the behavioral data; during the easy task subjects were better, faster and had overall better recognition when the task was on the angry person. Therefore, this seems to suggest that during the hard task there are not enough attentional resources left to process the threat which would be consistent with attentional load theory.

AMG is also affected by context; it responded only to negatively but not positively cued surprised faces (Kim, 2004). Previous studies showed that AMG respond not

only to threat presented in faces or bodies but also scenes. In Chapter 3 however, the AMG responded less to threatening than neutral scenes. Why this is the case is not clear. It did respond more to fearful than neutral faces in general.

■ Emotions in the future

Besides whole body movements, some more attention could be given in the future to investigating specific body parts. In a study by (Ousov-Fridin *et al.*, 2008), it was tracked at which parts people actually look when observing different static bodily expressions. Hereby it was found that subjects mainly focus on the hands when perceiving an angry or fearful body while when someone is happy, most attention goes to the face.

For facial expressions, a Facial Action Coding System has been developed decades ago (Ekman & Friesen, 1978) which tells us which facial muscles are involved in which expressions. Similarly, such a system should also exist for bodily expressions. Of course, in our society almost every part of our body is covered in cloths, which does not allow for different muscular tensions to be seen. Nonetheless, it is interesting to study this and progress is being made in our lab to develop such a Body Action Coding System.

Emotions are also an important topic in robotics. Emotional body movements should be measured in 3D to identify all parameters of human movement during basic emotions. In this way, believable avatars and robots can be created that express emotions that are easily recognizable by human perceivers. This affective computing can help us to build natural machine interfaces and obtain natural human-robot interactions.

It seems that brain areas involved in processing emotions show less response in *e.g.* schizophrenics and autistic individuals than healthy people. It would be rewarding to develop methods that can help them train their these areas, even though it is still a question whether this would also help them in understanding emotions better.

In the study of cultural differences, it is very important to add dynamics to the stimuli. Not just facial features are different between cultures, but real movements could make even more of a difference. Just think about the side-to-side head nodding of people from India, this is very typical to their culture.

Following up on the discussion that movement is inherent to emotions, an interesting study would be to show emotional movies of bodily expressions in a delayed way, or at different speeds, to see whether subjects still can recognize the different emotions. Furthermore, future studies need to focus on the timing of activation and the connectivity between the limbic system, body processing areas and higher cortical regions.

Emotion research is important and a good understanding of how facial and bodily expression recognition is processed in the brain is needed. Emotion recognition is

impaired in many clinical disorders such as autism or schizophrenia. Also because of its close link to motor processes, emotion is an important study object for many neurodegenerative genetic movement disorders like Huntington's and Parkinson's disease. Also, patients with anxiety or depression respond differently to emotional stimuli, but a good comprehension of and managing emotional input is necessary for being able to lead a normal life. Additionally, gender and personality differences should be taken into account in future studies since we clearly not all respond in exact the same way to the same emotions. Certainly, there is no doubt that much more research can and should be performed on the processing of emotional body language.

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Samenvatting en conclusies

Er gaat nagenoeg geen dag voorbij zonder dat we in contact komen met andere mensen, of het nou in het echte leven is of via de telefoon of het internet. Omdat we zulke sociale wezens zijn, zijn we echte experts geworden in het raden van andermans gevoelens ook al probeert men zijn ware intenties te verbergen. Dit is mogelijk door gespecialiseerde hersenmechanismen die geëvolueerd zijn over tijd.

Het werk beschreven in de voorgaande hoofdstukken had verschillende doelen. Eén daarvan was te kijken naar cultuurverschillen in het herkennen van gezichts- en lichaamsuitdrukkingen en of de sociale context een verschillende invloed heeft op die herkenning. Een ander doel was te kijken of de emotie van de context een invloed heeft op gezichtsverwerking in de hersenen. Een laatste doel was te onderzoeken of dreiging herkend kan worden slechts uit lichaamstaal alleen, ook al is de dreiging niet op de observator gericht en ook al zit de observator met zijn gedachten ergens anders.

In Hoofstuk 2 worden gedragsresultaten besproken die laten zien dat er cultuurverschillen bestaan tussen Nederlandse en Chinese studenten in hoe ze Caucasische gezichts- en lichaamsuitdrukkingen waarnemen. Chinezen hadden een slechter herkenningsgeheugen voor neutrale gezichten dan Nederlanders, maar zodra er emoties in het spel kwamen, waren ze even goed. Of dit komt omdat emoties ervoor zorgen dat gezichten beter opgeslagen worden of omdat ze hierdoor beter opgehaald kunnen worden, kan niet gezegd worden. Het laat wel zien dat emoties een speciale rol spelen. Voor verschillende match-to-sample taken waren Chinese langzamer dan Nederlandse studenten, met uitzondering van de gezichtsidentiteitstaken. Voor deze gezichten waren Chinezen sneller en accurater. Dit is een interessant resultaat omdat Aziatische landen meer collectivistisch zijn – in tegenstelling tot individualistische westerse landen – en mensen handelen daardoor meer conform aan de groep. Dit betekent dat ze proberen hun persoonlijke ideëen en intenties vaker te verbergen wat er misschien toe heeft geleid dat ze expert zijn geworden in het kijken naar gezichten om de ware intentie van mensen af te leiden. Ook hier weer, als emoties erbij betrokken worden, zijn de Chinezen even accuraat als de Nederlanders, alleen langzamer. Daarbij, wanneer lichaamsuitdrukkingen in een niet-sociale context beoordeeld moeten worden, kost ook dit Chinezen meer tijd. Alleen als de lichamen in een sociale context werden gepresenteerd, waren de Chinezen klaarblijkelijk sneller, en ook accurater. Het lijkt alsof de sociale omgeving hen een stimulans had gegeven om sneller en beter te presteren, wat wederom gerelateerd kan worden aan hun collectivistische maatschappij.

Hoofdstuk 3 laat zien dat angstige gezichten tot meer activatie in de fusiforme gyrus leidde wanneer de scene waarin ze gepresenteerd werden ook angstig was. Ditzelfde was

ook verwacht voor neutrale gezichten zoals gevonden in eerder electroencefalografisch onderzoek. Maar dit was hier niet het geval. Alhoewel, het is natuurlijk moeilijk om resultaten verkregen door verschillende hersenonderzoeksmethoden te vergelijken omdat ze verschillende processen meten. Gebieden in de hersenen die scènes verwerken reageerden minder op de scènes wanneer zij dreigend waren en ook wanneer er een gezicht in gepresenteerd werd. Dus zowel gezichts- als emotieverwerking lijkt scèneverwerking te verminderen, wat het belang van de eerste twee over de laatste laat zien.

Hoofdstuk 4 weidt uit over de dataset besproken in het voorgaande hoofdstuk, en laat zien dat extrastriate body area (EBA) reageert op dreigende scènes, ook al wordt er geen lichaam in gepresenteerd. Of dit komt door het zich voorstellen van mensen die wegvluchten of door eigen lichaamsgevoelens in reactie op de stimulus is open voor discussie. Het laat in ieder geval wel zien dat de functie van EBA nog niet zo duidelijk afgebakend is.

Voortbouwend op statische plaatjes van losse gezichten of lichamen naar dynamische stimuli, laat Hoofdstuk 5 zien dat de hersenen op dreigende situaties reageren ook al is de aandacht van de observator op een ongerelateerde taak. Gebieden die hier reageerden waren limbische gebieden zoals de amygdala (AMG), hypothalamus en hippocampus maar ook putamen en premotorische cortex die betrokken zijn bij actieobservatie en -voorbereiding. Deze resultaten illustreren het belangrijke actie-deel van emotie. Proefpersonen deden de ongerelateerde taak zelfs beter wanneer de situatie dreigend was. Wanneer dit het geval was, reageerden lichaamsverwerkingsgebieden in de fusiforme gyrus en superieure temporale sulcus ook meer op dreigende dan plagende interacties. De AMG lijkt een belangrijke rol te spelen in dit proces. Er is veel debat in de literatuur over of de AMG automatisch op dreiging reageert. In deze studie doet het dat, ook al is de dreiging niet gericht op de observator. Deze studie is ook conform eerdere studies naar inbeelding omdat dezelfde hersengebieden – zoals anterieure temporale pool, mediale prefrontale cortex, orbitofrontal cortex, en de temporoparietale kruising – geactiveerd waren tijdens het actief beoordelen van de intenties van de acteurs door de proefpersonen.

Voortbouwend op het belang van het herkennen van dreigende stimuli, laat Hoofdstuk 6 zien dat het focusen op een woedend persoon in een sociale interactie proefpersonen helpt om beter te preseteren op een ongelateerde taak. Aan de andere kant, de woedende persoon leidden hen af wanneer ze dezelfde taak uitvoerden op de andere, defensieve persoon. Alhoewel dit was alleen het geval wanneer er genoeg aandachtsbronnen over waren. Wanneer gefocused werd op een andere spatiële locatie en er op hetzelfde moment een hoge aandachtstaak uitgevoerd werd, had de dreiging geen invloed meer op gedrag. Ook reageerde de AMG meer wanneer

gefocused werd op de woedende dan defensieve persoon tijdens de makkelijk taak conditie. Dus er lijkt een grens te zitten aan hoe automatisch de AMG reageert op dreiging, en aandacht speelt hierbij duidelijk een rol. Observators hadden waarschijnlijk de minste lichamelijke gevoelens op de dreigende sociale interactie wanneer ze gefocused waren op de defensieve persoon en wanneer ze niet genoeg aandachtsbronnen over hadden zoals geimpliceert door de gevonden interactie in secundaire somatosensorische cortex.
Alles bij elkaar genomen, laten deze studies zien dat emoties een speciale invloed hebben op hersenprocessen; ze helpen het overkomen van het herkenningsgeheugen nadeel voor gezichten van een ander ras; als ze uitgedrukt worden in het lichaam van Caucasians worden ze net zo accuraat herkend door mensen van een Aziatische als een westerse cultuur; uitgedrukt in een scène hebben ze een invloed op gezichtsverwerking; en uigedrukt in een lichaam hebben ze een invloed op ons gedrag ook al worden we ingenomen door andere zaken en ook al zijn ze niet gericht op onszelf – tenminste, tot op zekere hoogte.

Emotie onderzoek is belangrijk en een goed begrip van hoe gezichts- en lichaamsuitdrukkingen worden verwerkt door de hersenen is nodig. Emotieherkenning is verstoord in vele klinische stoornissen zoals in autism en schizofrenie. Ook vanwege zijn sterke verbinding met motorische processen is emotie een belangrijk studieobject voor vele neurodegeneratieve genetische bewegingsstoornissen zoals de ziekte van Huntington en Parkinson. Daarbij, patienten met angst of depressie reageren anders op emotionele stimuli, terwijl een goed begrip van en het kunnen verwerken van emotionele input nodig is om een normaal leven te kunnen leiden. Ook zouden toekomstige studies rekening moeten houden met sekse- en persoonlijkheidsverschillen omdat we logischerwijs niet allemaal precies hetzelfde reageren op dezelfde emoties. Het is zeker dat er nog veel meer onderzoek kan en uitgevoerd moet worden naar het verwerken van emotionele lichaamstaal.

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Cirriculum Vitae

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Sinke, C.B.A., Kret, M.E., Van den Stock, J. & de Gelder, B. Cultural differences in recognition of facial and bodily expressions and contextual influence. (submitted)

Van den Stock, J., **Sinke, C.B.A.** & de Gelder, B. Threat sensitive body and scene perception. (to be submitted)

Sinke, C.B.A., Van den Stock, J., Goebel, R. & de Gelder, B. The influence of context on the processing of faces. (in preparation)

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"Wij zijn het aan onszelf verplicht om goed te leven, om kalmte en rust te vinden bij de dingen die we doen. Een zinvol leven leiden, dat is een meesterwerk waarop je trots kunt zijn."
~ Michel de Montaigne ~
(Les essais, Livre II, 1580)